CAMBRIAN EDRIOASTEROIDS FROM AUSTRALIA AND THE ORIGIN OF STARFISHES

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The early Middle Cambrian edrioasteroids *Stromatocystites reduncus* sp. nov. and *Edriodiscus primoticus* (Henderson & Shergold), and the median Upper Cambrian edrioasteroids *Chatsworthia spinosa* gen. et sp. nov., *Hadrodiscus parma* gen. et sp. nov. and *Cambroblastus enubilatus* gen. et sp. nov. are described. *C. enubilatus* is a primitive edrioblastoid linking edrioblastoids to the cyathocystinid Edrioasteroidea. *Chatsworthia* and *Hadrodiscus* are primitive isorophid edrioasteroids probably retaining biserial ambulacral flooring plates. The primitive starfish *Archegonaster*, from the Llanvirn of Czechoslovakia is redescribed. It is shown to be sufficiently generalised in its morphology to belong to the common stem lineage of both asteroids and ophiuroids. The most probable ancestry of *Archegonaster* is traced to Cambrian edrioasteroids with *Edriodiscus* as its closest relative. The origin and homologies of the ophiuroid jaw are clarified on the basis of *Archegonaster* mouth elements and it is argued that mouth angle plates are homologues of first ambulacral ossicles and the torus and its mouth spines are homologues of the first adambulacral ossicles and its spines.
Edrioasteroid phylogeny is analysed using numerical cladistic methodology and an evolutionary tree constructed from stratigraphical occurrence data. Edrioasteroids diversified in paleoecological terms from being unattached low-level epibenthic suspension feeders to fill a number of different niches during the Cambrian and Early Ordovician. Different groups became semi-infaunal, vagile, semi-permanently attached or permanently cemented to a hard substratum, while one line even became convergent with crinoids by evolving a stem. The fauna described here suggests that edrioasteroids continued to diversify through the Upper Cambrian and that their rarity at this time interval is due to preservational factors.
☐ *echinoderms, Cambrian, Ordovician, Australia, Czechoslovakia.*

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Echinoderms have a good fossil record that extends back to the Lower Cambrian and possibly even into the Precambrian (Gehling, 1988). Much attention has been focused recently on the early evolutionary history of this group (Termier & Termier, 1969: Ubaghs, 1975; Paul, 1977, 1979, 1988; Sprinkle, 1976, 1980a, 1981; Paul & Smith, 1984; Smith, 1984, 1986, 1988a; Campbell & Marshall, 1987). This has greatly improved our understanding of the morphology of early, primitive echinoderms but substantial gaps remain in our understanding of both phylogenetic relationships and evolutionary patterns as echinoderms diversified. In particular the origins of certain post-Cambrian lineages remains problematic because suitable intermediates, linking the derived forms to known Cambrian fauna, have not been discovered. Two factors greatly aggravate this problem; the apparent absence of a good Upper Cambrian record for echinoderms and the strong geographical bias in the known early fossil record.

The dearth of identifiable Upper Cambrian fossil echinoderms was first pointed out by Sprinkle (1976) who noted that, although disarticulated elements of echinoderms were not uncommon in Upper Cambrian limestones of western U.S.A., whole animals were extremely rare. Sprinkle (1980a, 1981) and Campbell & Marshall (1987) argued that this low diversity is genuine and that echinoderms underwent a two phase diversification, as postulated for marine invertebrates in general (Sepkoski, 1979). Smith (1988a), however, interpreted the Upper

Cambrian as a period of preservation failure because although many Ordovician lines could be traced back to Middle Cambrian antecedents, few had described representatives from the Upper Cambrian. Of 80 species known from the Cambrian, only 12 (15%) are Upper Cambrian and of these, only 7 have formally been described. Similarly, of 40 named Cambrian genera only 7 (17.5%) come from the Upper Cambrian. Upper Cambrian echinoderms are thus considerably under represented.

A second problem that is rarely considered is the strong geographical bias of the fossil record towards North America and western Europe. For Cambrian echinoderms 46 species occur in North America, 26 in Europe, 7 are Australian and one each is known from the U.S.S.R. and North Africa. Thus, excluding one species common to both areas, 71 out of 80 (87.5%) species come from Europe and North America and only 9 (12.5%) from elsewhere in the world. This disparity must surely reflect the considerably greater amount of research effort that has been spent investigating Cambrian outcrops in western Europe and North America. Thus, although we may now have a fairly good idea of echinoderm diversity in the Cambrian of Europe and North America, there is great scope for new discoveries in suitable Cambrian sequences elsewhere in the world.

Because Cambrian faunas outside Europe and North America are less well studied and because one of the few Upper Cambrian echinoderm-bearing beds is in Queensland, Australia, we felt that a search for echinoderms in the Cambrian of western Queensland might be highly rewarding. This paper is a direct result of a two-week field collecting trip and describes the edrioasteroid species that were discovered. A new carpoid from the Upper Cambrian of Queensland will described elsewhere (Smith & Jell in prep.). In addition we give a description of the primitive asteroid/ophiuroid antecedent *Archegonaster pentagonus* Spencer,1951 from the Lower Ordovician of Czechoslovakia, as this has bearing on the phylogenetic diversification of Cambrian edrioasteroids.

The first Australian Cambrian echinoderms described were *Cymbionites craticula* Whitehouse, 1941 and *Peridionites navicula* Whitehouse, 1941 from the early Middle Cambrian Thorntonia Limestone, north of Mount Isa, western Queensland. These were subsequently considered (Smith, 1982) to be the basal circlet of two different eocrinoids and our collecting at the type locality in May 1989 confirms this view. In 1971 Henderson and Shergold described *Cyclocystoides primotica* from the early Middle Cambrian Beetle Creek Formation, associated with *Redlichia* spp. This species is not a cyclocystoid (Jell *et al.*, 1985; Smith, 1986; Smith & Paul, 1982) and has been reassigned to the Edrioasteroidea and placed in its own genus *Edriodiscus*; it is elaborated upon below. Fleming (1977) showed the great abundance of dissociated echinoderm plates in the Lady Annie and Duchess phosphate deposits in the early Middle Cambrian Beetle Creek Formation, but made no taxonomic identifications. This material, collected from the vicinity of BMR locality D640 (Fig. 1), contains abundant, well-preserved disarticulated plates of edrioasteroids and is currently under investigation. Most of our knowledge of Australian Cambrian echinoderms derived from the work of Jell *et al.* (1985) who described *Cambraster tastudorum* and *Ctenocystis jagoi* from the medial Middle Cambrian part of the Catecna Group in northern Tasmania, isolated plates of *Cambraster* and probably *Gogia* from the early Middle Cambrian Coonigan Formation in western New South Wales, *?Stromatocystites* sp. (=*S. reduncus* sp. nov. below) from the type locality of *E. primotica*, and the eocrinoid *Ridersia watsonae* and an unnamed isorophid (=*Chatsworthia spinosa* gen. et sp. nov. below) from the medial Late Cambrian Chatsworth Limestone near Chatsworth Homestead, 100 km north of Boulia, western Queensland. Thus the five taxa described below represent half of the known Cambrian echinoderm fauna of Australia.

GEOLOGICAL SETTING OF LOCALITIES

The Cambrian fauna described here comes from the eastern portion of the Georgina Basin in western Queensland (Fig. 1). Sedimentation in this epicontinental basin occurred from the late Precambrian to the Devonian, although not continuously in any one area. Although the entire basin has been mapped geologically at a 1:125,000 scale, more detailed mapping has been confined to a few areas within the basin, mostly areas that were prospected for phosphate deposits in the 1960s and 1970s. The Burke River structural belt in the southeast has received considerable attention and the biostratigraphy of the echinoderm bearing Upper Cambrian Chatsworth Limestone in the area south of Lily Creek (Fig. 1) has been studied in great detail by

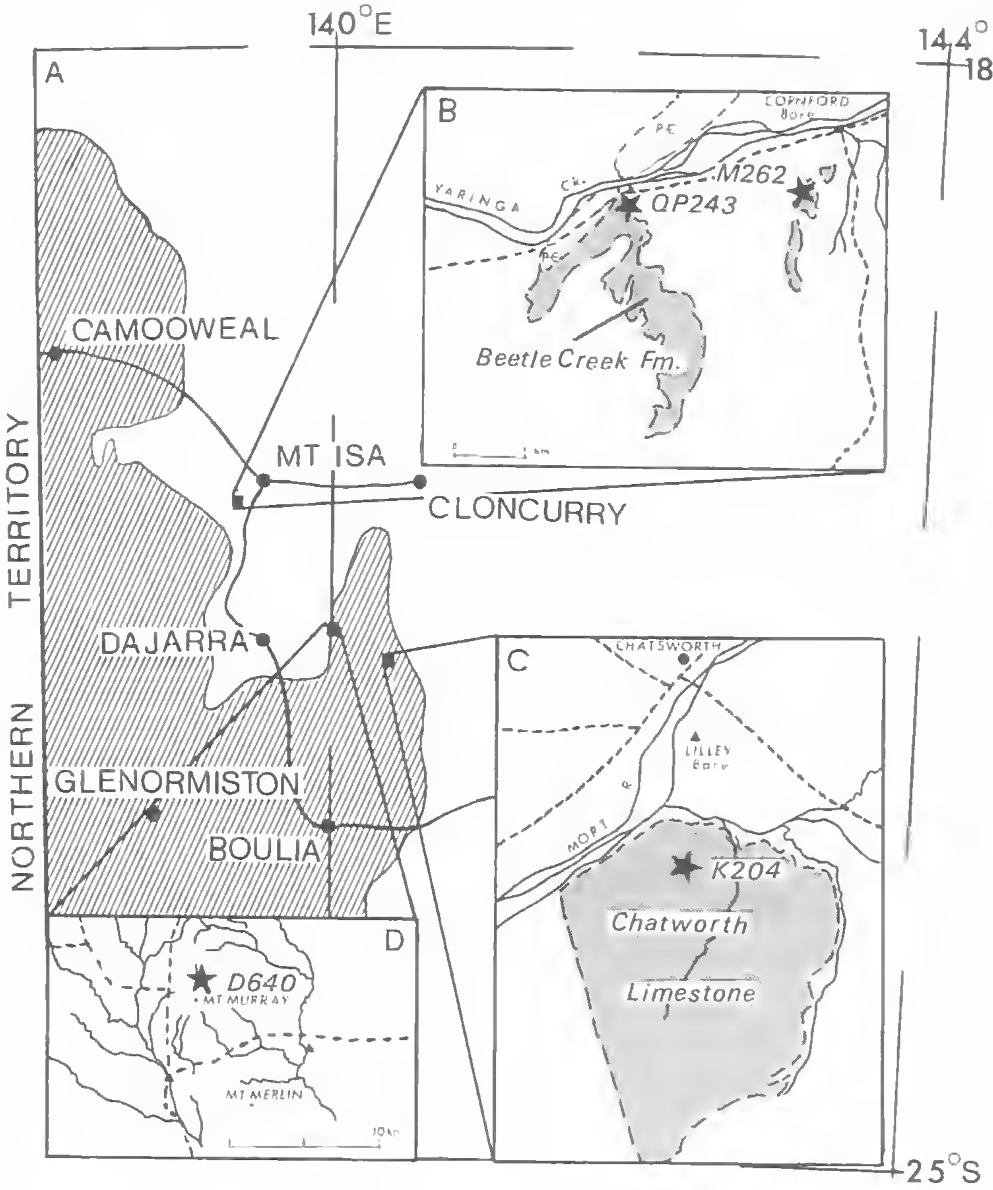
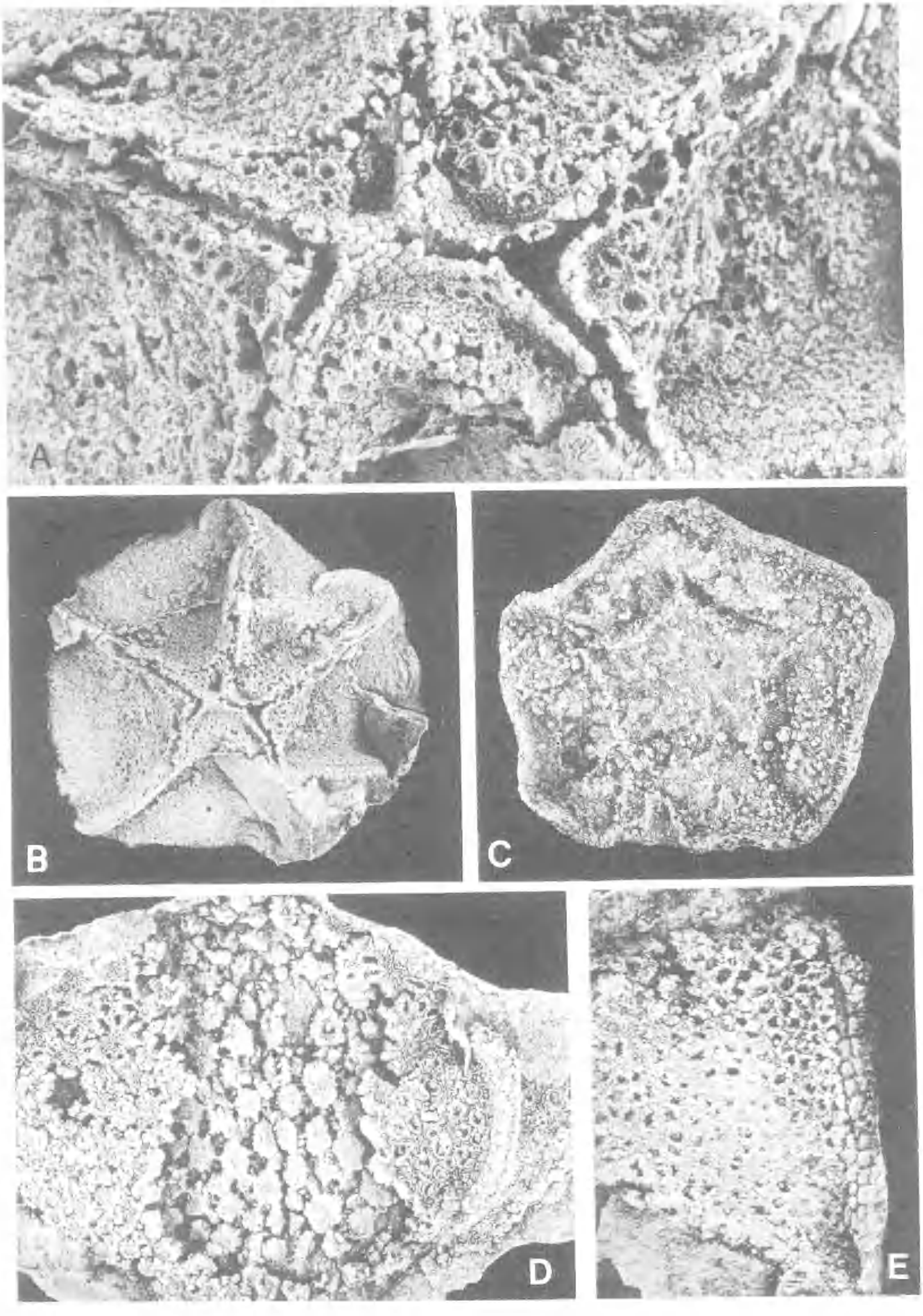


FIG. 1. Locality map. A, showing extent of Cambrian outcrop in the Georgina Basin (diagonally lined), main roads, and centres of population in far western Queensland (redrawn from Smith, 1972). B, Cornford Bore area on Yaringa Creek (from Henderson & Shergold, 1971). C, Chatsworth area (from Shergold, 1982; scale same as in B). D, Mount Murray area (from Jones & McKenzie, 1980). Triangles = water bores; stars = fossil localities mentioned in the text.

Shergold (1982). He recorded pelmatozoan debris from a number of horizons and, at his locality K204, the eocrinoid aff. *Macrocystella* sp. That fossil was later described as *Ridersia watsonae* by Jell *et al.*, (1985), together with two specimens of an indeterminate isorophid edrioasteroid. Further collecting by the authors at that locality has yielded many more specimens of *Ridersia watsonae*, the edrioasteroids *Chatsworthia spinosa* and *Hadrodiscus parma* and the edrioblastoid *Cambroblastus enubilatus*.

Shergold (1982) described the Chatsworth Limestone in its type section, south of Lily Creek, as 'dominantly sandy or silty pelletal skeletal grainstone and packstone, with subordinate wackestone and clast grainstone; the environment of deposition was high energy, shallow subtidal, intertidal and possibly aeolian;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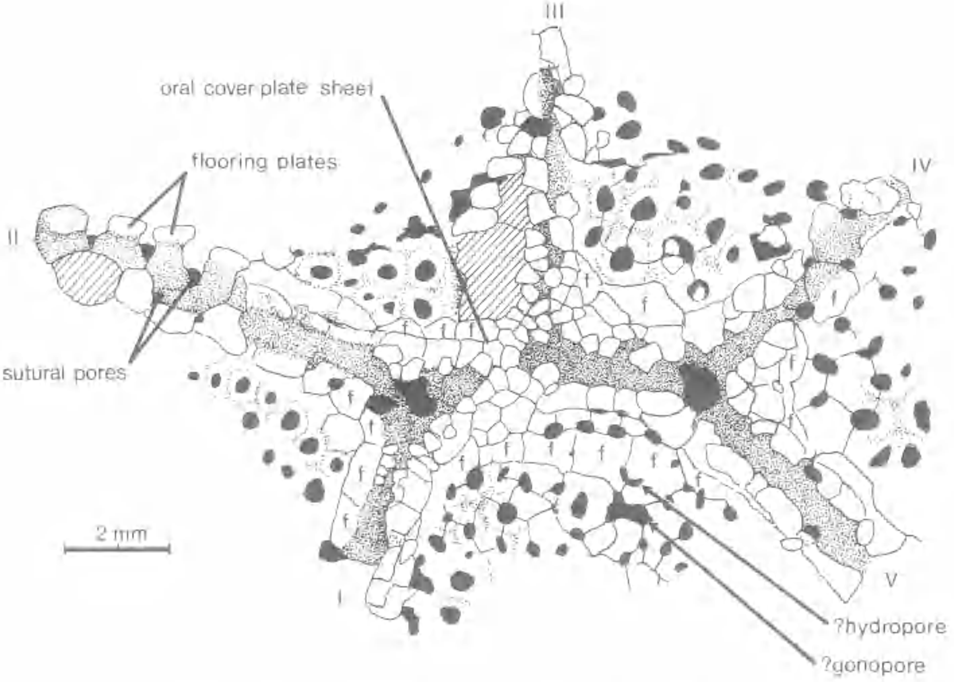


FIG. 3. *Stromatocystites reduncus* sp. nov.; camera lucida drawing of plating in the oral region of the holotype. f = flooring plate; ambulacra numbered I-V.

cross-lamination and ripple marks are common; trilobites and echinoderms are predominantly dissociated and fractured skeletal parts are not uncommon; current winnowing and alignment of organisms widespread.' Horizon K204 refers to a 4 m thick unit of thin-bedded limestone which is a pelletal grainstone containing rare ooids (Shergold, 1982, p. 97). Cross lamination occurs throughout this unit and shallow but large-scale channeling results in individual beds having limited lateral extent. Current alignment of fossils is often evident and we discovered a shallow channel infill, about 2 m by 1 m, with about 100 adult specimens of *Ridersia watsonae* lying in parallel alignment. Obvious hardground surfaces are absent. In addition to the echinoderms listed above, the fauna includes the trilobites *Iveria iverensis*, *Connagnostus* sp., *Peichiashania secunda*, *Prochuangia glabella*, *Pseudagnostus parvus* and *Wuhuia silex*, inarticulate and articulate brachiopods, monoplacophorans, gastropods, sponges and an undescribed cothurnocystid. Shergold (1982) placed this horizon within his *Peichiashania secunda/Prochuangia glabella* Assemblage Zone at the top of the Idamean Stage, which he correlated internationally with the middle Franconian of North America.

The second locality from which we describe Cambrian echinoderms lies to the west of Mount Isa. At BMR locality QP243 (Fig. 1) on a low rise some 500 m south of Yaringa Creek at the bore some 3 km west of Cornford Bore situated on the north of Ardmore Station, 45 km west-southwest of Mount Isa (20° 49.5' S, 139° 03.5' E) Henderson & Shergold (1971) discovered a single specimen with two individuals of *Edriodiscus primoticus*. Here, laminated chert with silicified coquinite, algal chert and siltstone form the lower part of the Beetle Creek Formation, resting unconformably on Precambrian quartzites. Accompanying these rare echinoderms are abundant exoskeletal fragments of the trilobite *Redlichia*. Öpik (1970) described from this horizon at the nearby M262 (Fig. 1) the species *Redlichia versabunda*, *R. vertumnia* and

FIG. 2. *Stromatocystites reduncus* sp. nov., early Middle Cambrian from QP243 near Cornford Bore. A-C, QMF17914, holotype. A, oral area, x7 (see Figs 3, 4A). B, oral surface, x1.7. C, aboral surface, x1.7. D. BMNH E63523, paratype, detail of oral surface with ambulacrum, margin of disc at bottom x3. Oral plating has been lost from the central band to reveal the internal surface of aboral plates. E, QMF17920a, paratype, detail of oral surface showing interambulacral plating and, on the right hand margin, ambulacral flooring and cover plates, x3 (see Fig. 4B). All latex casts whitened with ammonium chloride sublimate.

R. mayalis, and all three described morphologies are recognizable amongst our collection from QP243. Öpik dated the horizon as late Ordian, immediately older than his *Redlichia chinensis* Zone, and early Middle Cambrian.

A further specimen of *Edriodiscus primoticus* was collected and described by Jell *et al*. (1985) from this locality and on the same slab there was also a fragment of a *Stromatocystites* sp. We recollected from this locality and extended our search some 400-800 m further south along the ridge with QP243 at its northern end. This resulted in the discovery of an additional 35 specimens of the *Stromatocystites* and 5 specimens of *Edriodiscus primoticus*, described below. They occur in distinct layers associated with much disarticulated trilobite material.

REPOSITORIES OF MATERIAL

The material described below is housed in the following institutions: British Museum (Natural History), London [BMNH]; Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra [CPC]; Narodní Museum, Prague [NM]; Museum of Victoria, Melbourne [NMVP]; Queensland Museum [QMF]

SYSTEMATIC DESCRIPTIONS

Class EDRIOASTEROIDEA Billings, 1858

Stromatocystites Pompeckj, 1896

TYPE SPECIES

Stromatocystites pentangularis Pompeckj, 1896; Middle Cambrian of Czechoslovakia and late Lower Cambrian of Newfoundland.

DIAGNOSIS

Edrioasteroids with fully plated aboral surface approximately as large as the oral surface. Undifferentiated oral mouth frame and cover plate series; biserial flooring plates and multiserial cover plate series. Interambulacra with well developed epispires. No differentiated peripheral rim plates. Interior of aboral surface with a series of divaricating ribs radiating from a central platform of larger plates.

OTHER SPECIES

S. walcotti Schuchert, 1919 (late Lower Cambrian of Newfoundland). *S. reduncus* sp. nov. (early Middle Cambrian of Australia).

REMARKS

Stromatocystites is the oldest and most primitive edrioasteroid known and is a possible antecedent to all later edrioasteroid groups. The absence of differentiated peripheral rim plates separates *Stromatocystites* from most other edrioasteroids and appears to be primitive for the class, as is the presence of epispires in interambulacra and the completely plated aboral surface. Although both previously known species have straight ambulacra, the new species described below has curved ambulacra. This is also the condition seen in the even more primitive Lower Cambrian *Camptostroma* (Paul & Smith, 1984), although the direction of curvature is not the same.

Stromatocystites reduncus sp. nov.
Figs 2-9

?*Stromatocystites* sp. Jell, Burrett & Banks, 1985, p.192, figs 7c-f, 8.

ETYMOLOGY

From Latin *reduncus* curved back, in reference to the shape of the ambulacra.

MATERIAL

Holotype QMF17914 part & counterpart; paratypes, QMF17915-25, 17938, 17944, BMNH E63519-22, E63525. Other material QMF17926-37,17939-43, 17944, BMNH E63523, 63524, NMVP107478.

AGE AND OCCURRENCE

From chert beds of the Yelvertoft Member, Beetle Creek Formation, early Middle Cambrian, exposed on the northern flank of a low rise 400-800 m south of the bore at Yaringa Creek, 50 km west-southwest of Mount Isa, Western Queensland (GR 980965).

DIAGNOSIS

A *Stromatocystites* with distally recurved ambulacra; ambulacra I and V curving clockwise, ambulacra II, III and IV anticlockwise.

DESCRIPTION

Specimens reach 53 mm in diameter and are rounded pentagonal in outline (Fig. 2B,C). The lower (aboral) surface is flat or slightly concave while the oral surface is moderately convex. Both surfaces are fully plated and there is no sharp demarcation separating oral from aboral surface or any distinct peripheral rim plating.

Ambulacra are long and slender, forming sharp, well-defined ridges over the oral surface and meeting centrally in a 2:1:2 arrangement (Figs 2A, 3). They are straight proximally but close to the edge of the oral surface they curve sharply so that the tips of the ambulacra come to face centrally (Figs 2B, 5C,D). Ambulacra I and V curve clockwise and ambulacra II, III and IV curve anticlockwise. The recurved portion is about 1/3 of the radius in larger specimens. Flooring plates are biserially arranged (Figs 2A, 3). They are rather broad and short and there are large marginal sutural pores between adjacent flooring plates that almost reach the perradial suture. These pores lead to the interior of the theca. The outer edge of the flooring plates is exposed along the adradial margin of the ambulacra (Figs 2E, 3, 4A,B) where they appear as a row of rectangular plates. Flooring plates are more fully exposed towards the distal ends of the ambulacra. Each flooring plate carries a large primary cover plate which is broader than tall with a blunt distal point. These cover plates sit directly on top of the flooring plates. Above the primary cover plates there is a sheet of smaller secondary cover plates without regular arrangement (Figs 2D, 4A,B). These are in two or three irregular rows and are about 1/3 the size of the primary cover plates or less. Ambulacral plating decreases in size towards the arm tips.

In the oral region the ambulacral series is undifferentiated (Figs 2A, 3). There are no enlarged flooring or cover plates and there appear to be four flooring plates along the posterior border of the oral area (Figs 2A, 3). The cover plate sheets continue across the oral area without differentiation. In the flooring plate closest to ambulacrum V there is a crescentic opening which might represent the hydropore and a more ragged opening that might be the gonopore (Figs 2A, 3).

Interambulacral areas are broad and composed of many plates. Towards the centre the plates are large (1-1.5 mm diameter) and stellate in outline with prominent epispires surrounded by a rim (Figs 2A, 3). The remainder of the plate surface has a reticulate ornament but the rim and inner walls of the epispires are smooth (Figs 2D,E, 4C). The largest epispires (up to 0.5 mm diameter) are found centrally in each interambulacrum where they are oval in outline. Epispires decrease in size towards the margin of the oral surface and are more angular, either slit-like or, where developed at triple suture junctions, triangular in outline. Interambulacral plates are smooth internally and have nearly vertical sutures (Fig. 6A,B).

The periproct is a cone of lath-shaped plates, some 20-30 in number, situated close to the margin on the oral surface mid-way between the two posterior ambulacra (Figs 2B, 5C, 6B). Epispires reduce in size close to the periproct and are absent from the cone of lath shaped plates forming the periproct.

There is no differentiated peripheral rim or marginal frame. At the edge of the theca, interambulacral plates become progressively smaller and rapidly merge into a narrow zone of small granular ossicles lying subambitally (Figs 5B, 7A,B, 8). This 2-3 mm wide band usually stands out as an elevated rim when seen from the aboral surface, suggesting that there might be some

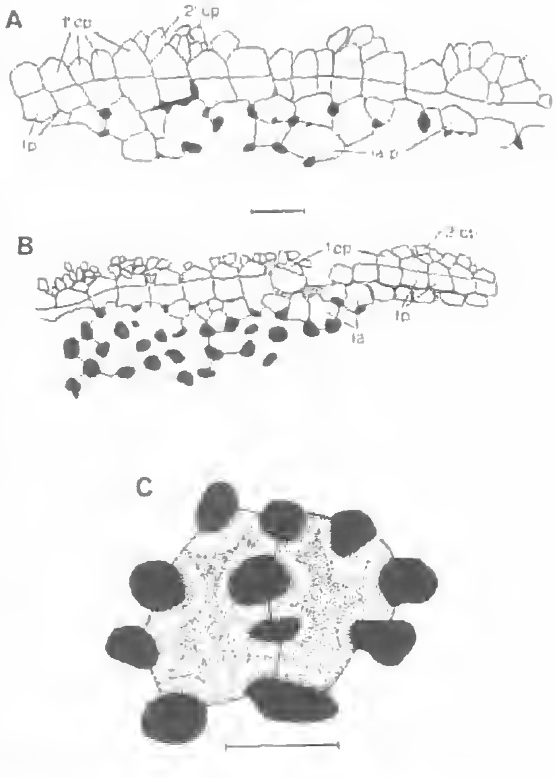
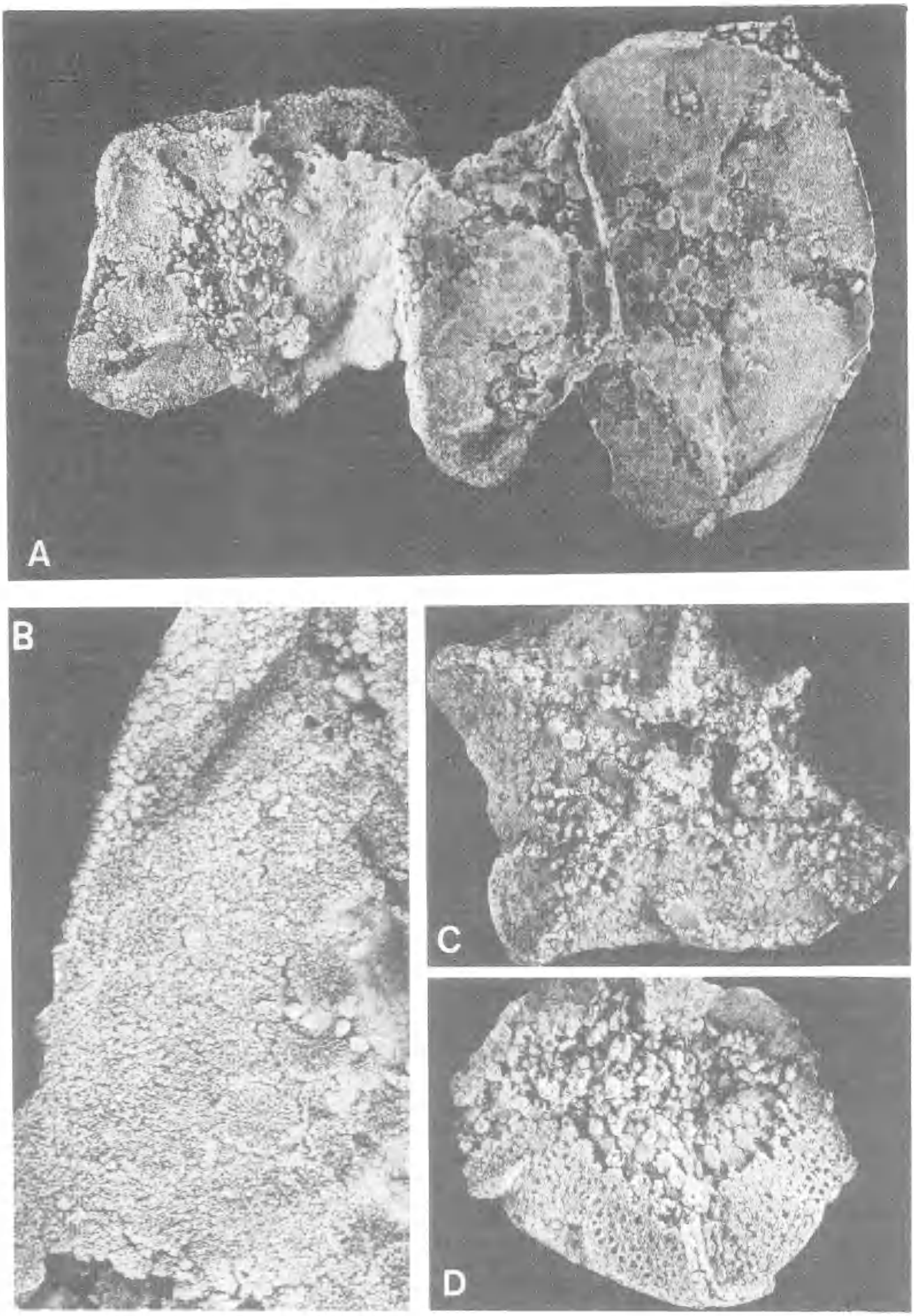


FIG. 4. *Stromatocystites reduncus* sp. nov.; camera lucida drawings of plating. A, QMF17914a, holotype; lateral view of ambulacrum V at mid-length. B, QMF 17920a, lateral view of ambulacral plating. C, QMF17927, two oral interambulacral plates in external view. cp = cover plate; fp = flooring plate; Ia p = interambulacral plate; 1° = primary; 2° = secondary. Scale bar = 1 mm.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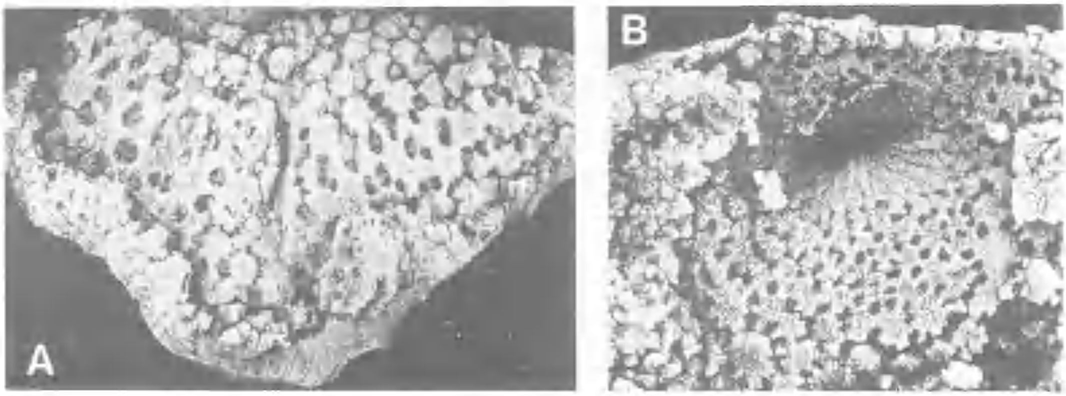


FIG. 6. *Stromatocystites reduncus* sp. nov. A, QMF17924, paratype, internal surface of aboral plates towards the margin of the disc, x3.5. B, QMF17944, paratype, internal surface of oral plating in posterior interambulacrum with lath-like plates of the periproct evident, x4. Latex casts whitened with ammonium chloride sublimate.

weak development of peripheral plates internally forming a more robust frame to the theca.

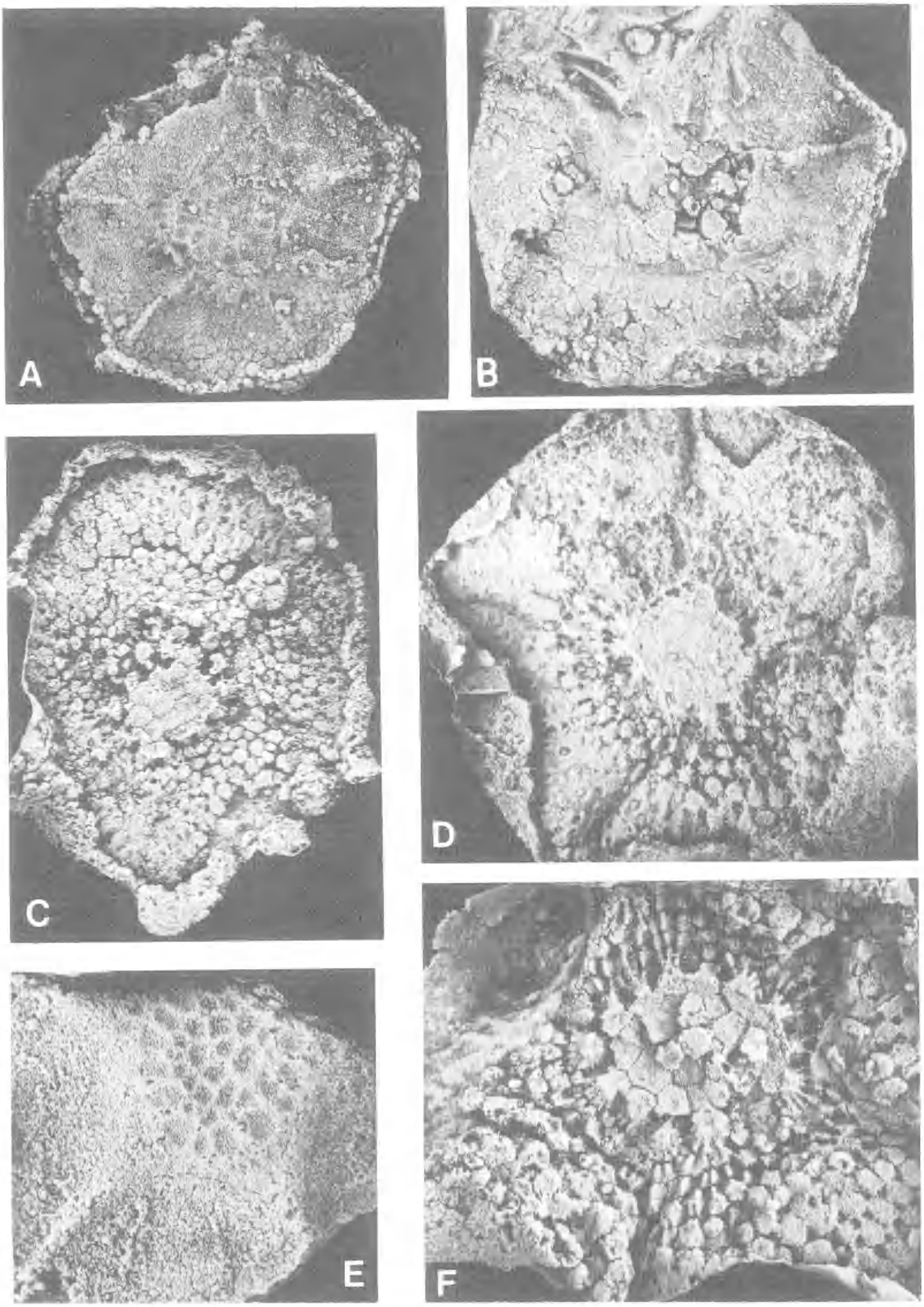
On the aboral surface, inside the marginal zone of granular plates, the majority of the surface consists of a pavement of oval to sub-polygonal plates surrounded by rings of small granular ossicles (Figs 5A,B, 7A,B, 8). The large plates are 1.5-2 mm in diameter and become larger towards the centre. They have a distinctive reticulate pattern of fine radiating ribbing (Fig. 5B). At the centre there is a small region of larger plates lacking interspersed granular plates around their borders. These are in no particular arrangement and there is no clear central plate (Figs 5A, 7A,B,E, 8). The interior of the aboral surface is very distinctive. There is an outer zone composed of rather thick stellate plates, resembling the epispire-bearing plates of the oral surface (Figs 2D, 6A). However, the spaces between the large plates are filled with small, thin platelets that appear deep down in the depressions. This outer zone is best developed interradially. Towards the centre, plates develop pronounced sharp keels that run radially and occasionally branch and merge (Figs 7C,D,F, 9). This zone of ribbed plates is extended radially to create a stellate pattern. Ribbing becomes stronger towards the centre and ends against an elevated platform of some 12-15 large polygonal plates bounded by a low peripheral ridge (Figs 7C,D,F, 9). The plates around the edge of this platform have radiating ridges on their distal half, between 2 and 6 major ridges per plate (Fig. 9). These ridges are continuous with the radial ribs on the more distant plates. The outer boundary of internally ribbed aboral plates corresponds to the elevated pentagonal area that is seen from the exterior.

REMARKS

The incomplete specimen of Jell *et al.* (1985, figs 7C-F, 8B) from this locality could only tentatively be assigned to *Stromatocystites*. Jell *et al.* (1985) noted the internal ridging to aboral plates which had previously been unrecorded from any stromatocystitid. However, we now know that a similar, but less well-developed, system of ridges occurs internally in the type species, *S. pentangularis* (Fig.10). Re-collecting from this locality has produced a further 35 specimens and it is now the best known of all *Stromatocystites* species. It differs from the other two species of *Stromatocystites* in having distally curved ambulacra.

The oral area of the holotype is well-preserved and allows the plating of this region to be described in detail for the first time in *Stromatocystites*. The crescentic opening here tentatively identified as the hydropore lies across a suture between two flooring plates and thus

FIG. 5. *Stromatocystites reduncus* sp. nov. A,B, QMF17916, paratype. A, aboral surfaces of two individuals, x1.4. B, detail of external ornament on aboral plates, x4. C, BMNH E63519, paratype, oral surface showing ambulacra I and II, and the periproct, x2. D, QMF19738a, paratype, oral surface in external aspect with two curved ambulacra and, in the upper half, the interior of the aboral surface, x2. Latex casts whitened with ammonium chloride sublimate.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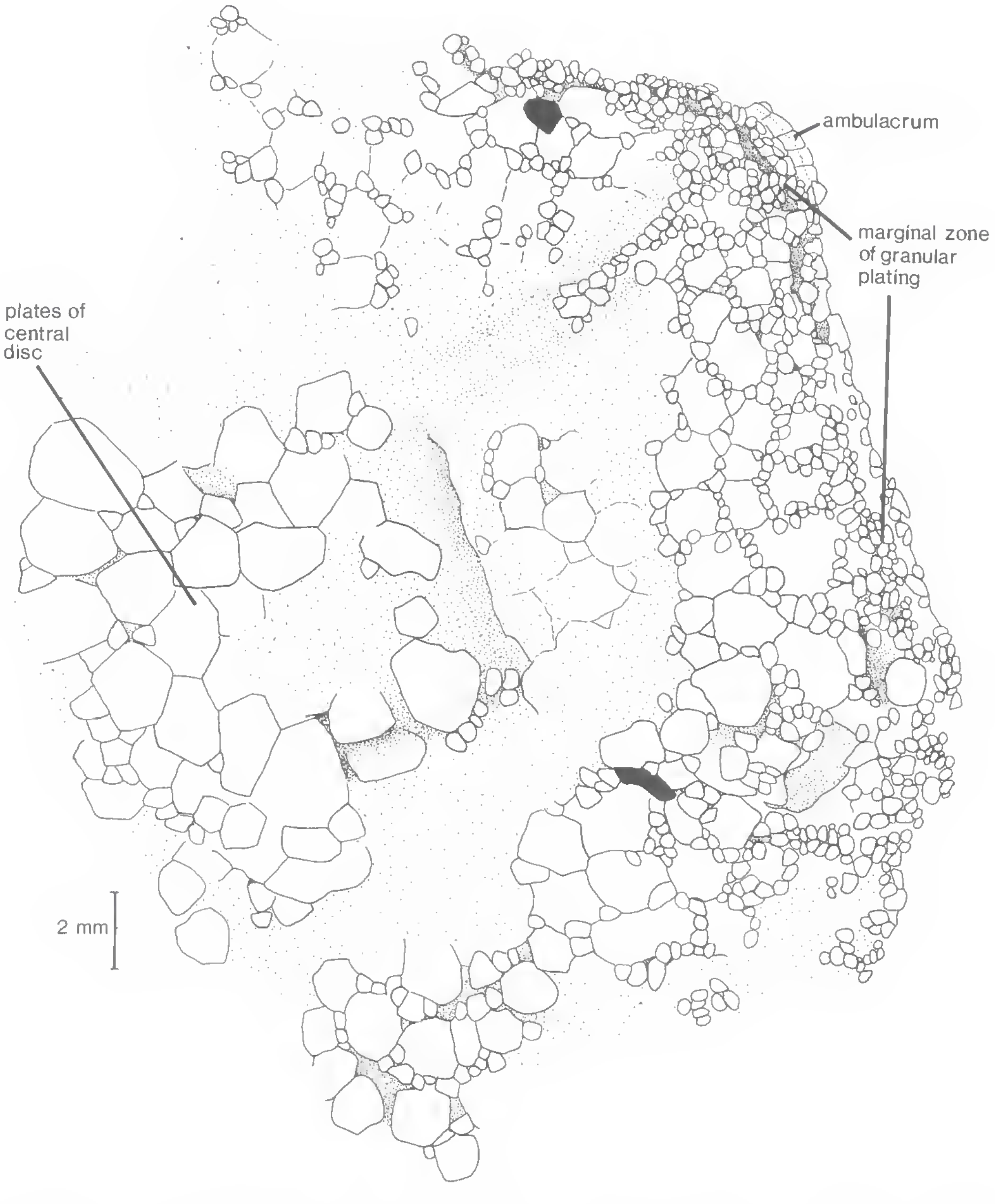


FIG. 8. *Stromatocystites reduncus* sp. nov., QMF17925, paratype, camera lucida drawing of plating on the exterior aboral surface.

FIG. 7. *Stromatocystites reduncus* sp. nov. A, BMNH E63522, paratype, aboral surface, exterior, x2. B, QMF17925, paratype, aboral surface, external, x1.8 (see also Fig.8). C, QMF17917a, paratype, aboral surface, interior, x2.3. D, BMNH E63521, paratype, aboral surface, interior, x1.7. E, QMF17919a, paratype, aboral surface, exterior, showing the central zone of larger plates towards the top, x3. F, QMF17915, paratype, aboral surface, interior, central part only, x4 (see also Fig. 9). Latex casts whitened with ammonium chloride sublimate.

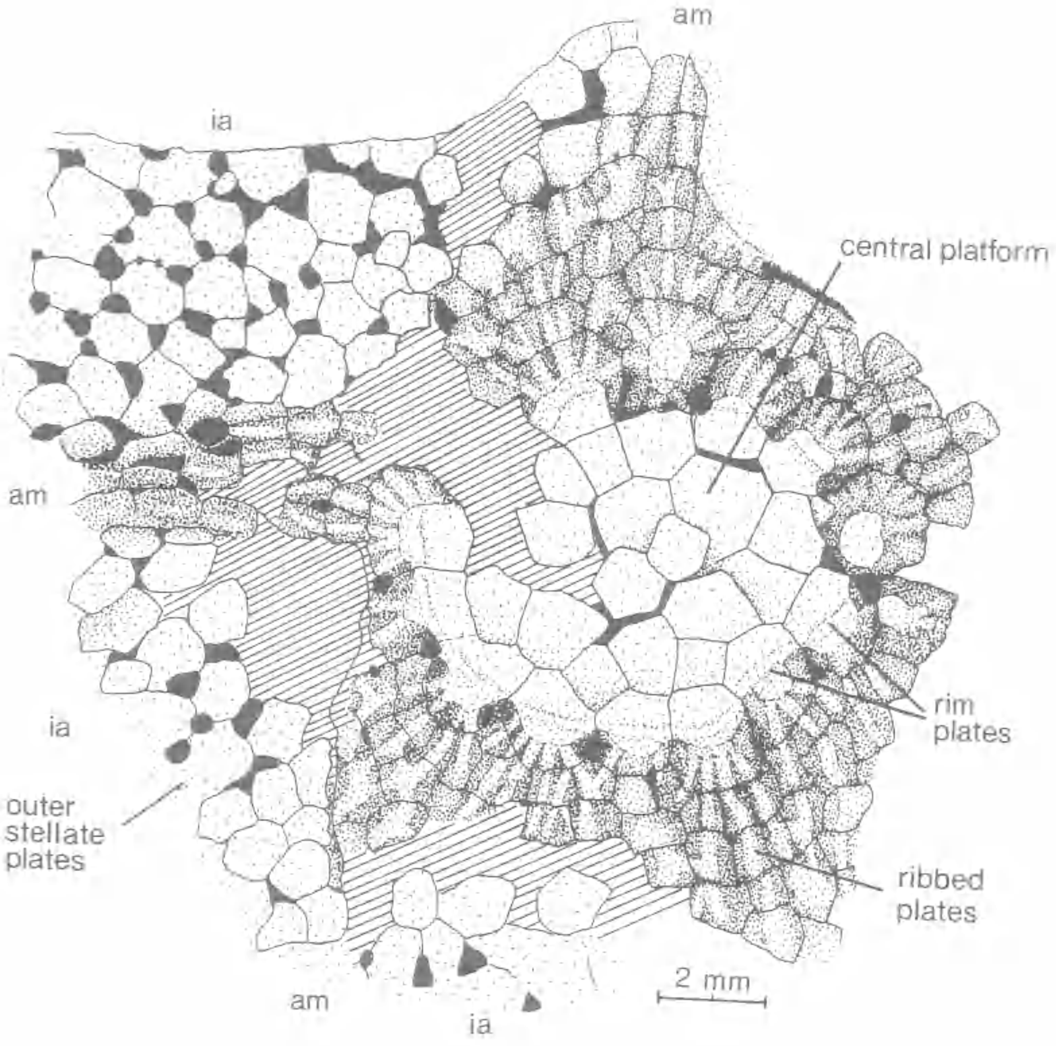


FIG. 9. *Stromatocystites reduncus* sp. nov., QMF17915, paratype, camera lucida drawing of plating in internal aspect of the aboral surface (see also Fig. 7F). am = ambulacrum; ia = interambulacrum.

resembles the arrangement in *Totiglobus* (see Bell & Sprinkle, 1978) and edrioasterids. The central part of the oral area was roofed over by what appears to have been a continuous cover plate sheet and it seems probable that the mouth was permanently covered in *S. reduncus*. An unusual feature of the oral area is the set of four small oval holes in the cover plate sheet of the posterior interray.

The aboral system of internal ridges radially arranged around a central platform of plates is particularly intriguing from a functional point of view. A similar arrangement is seen in *Totiglobus*, although its entire aboral surface is reduced to a small disc and the ridges occupy virtually the entire outer part. In *Stromatocystites* the exterior of the aboral surface usually shows a central stellate region that is elevated above the more peripheral interradial zones and the outline of this elevated region corresponds to the outer border of the internally ribbed region. The invaginated appearance of interradial zones on the aboral surface and the radial arrangement of the surrounding ridges suggests that this structure might be developed for adhesion. The disc of *Totiglobus* undoubtedly had to have had some form of aboral adhesive disc since its globose shape would have made it very unstable otherwise. Thus

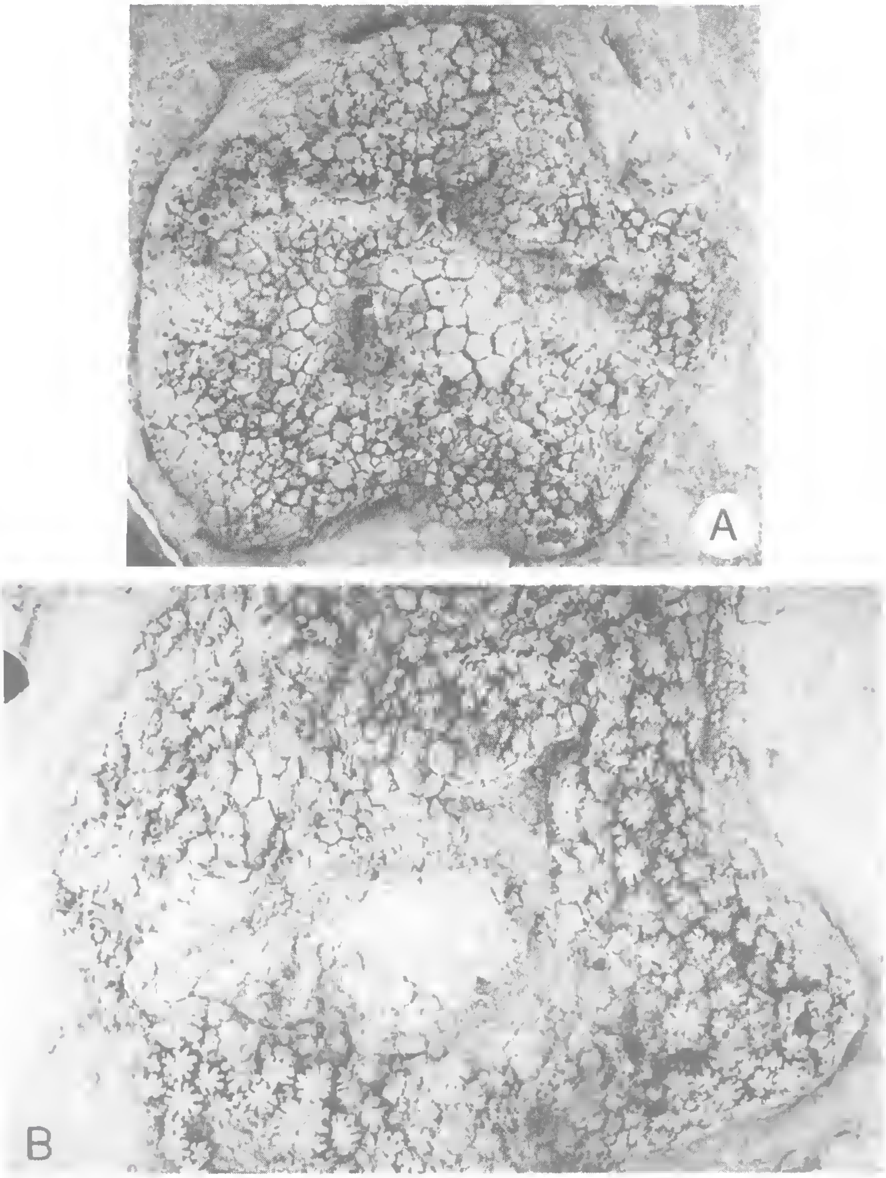
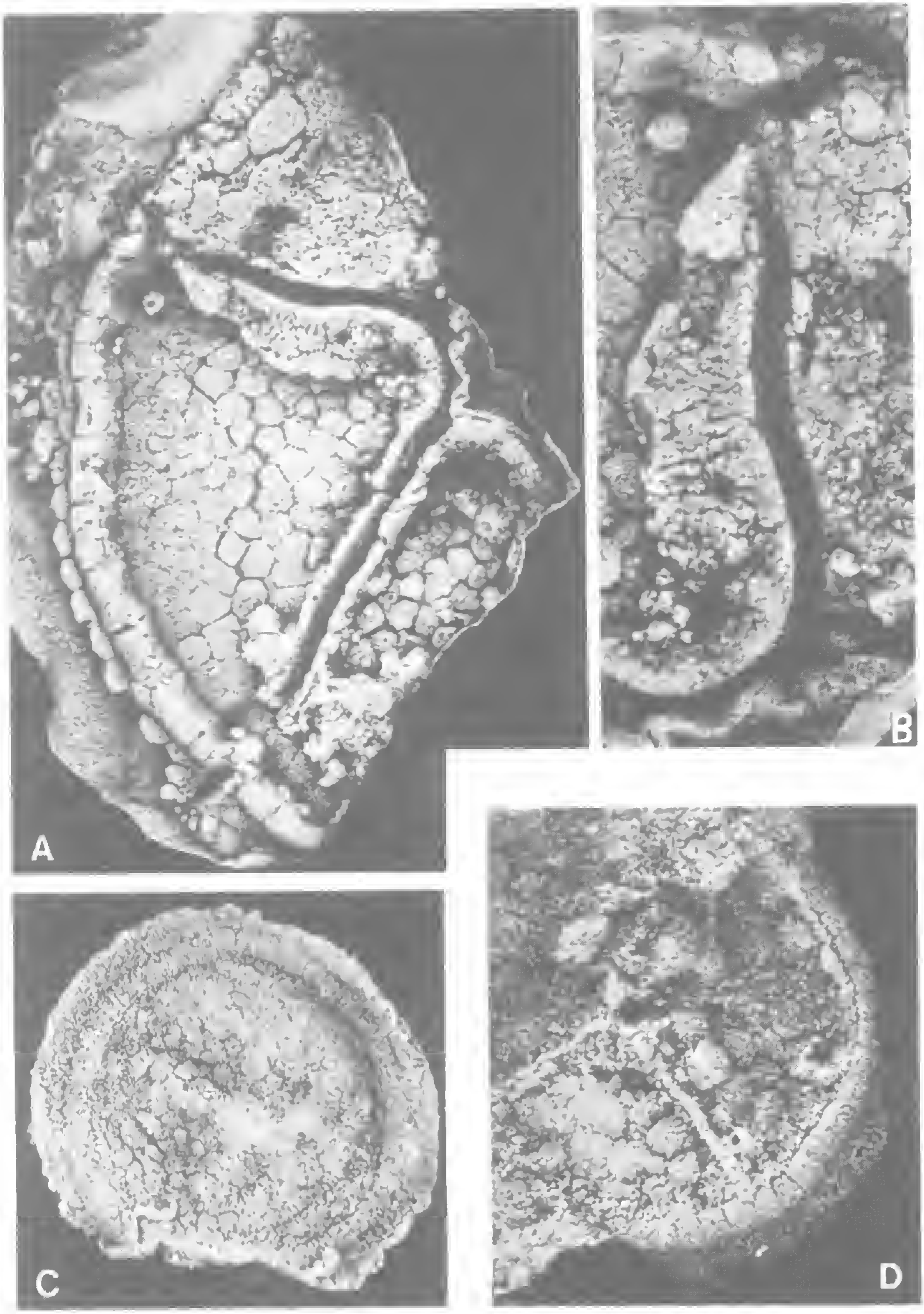


FIG. 10. *Stromatocystites pentangularis* Pompeckj, New York State Museum E1673, from the Middle Cambrian of Ginetz, Czechoslovakia. A, aboral surface, exterior, showing the central zone of large polygonal plates, x3. B, aboral surface, interior, of a second specimen showing the central platform surrounded by a stellate zone of ribbed plates, x3. Latex casts whitened with ammonium chloride sublimate.

it seems reasonable to interpret the aboral internal structures in Stromatocystites as part of an adhesive disc. We suspect that the ridges mark the site of attachment for radial muscles and that these muscles were employed to elevate the central part of the disc to create a suction pad. The distal attachment point for the muscles is, however, weakly developed in *Stromatocystites*, although in *Totiglobus* there are stout peripheral rim plates to which muscles could attach. Possibly a marginal frame of peripheral rim plates arose to provide rigidity and to secure anchorage for the radial aboral muscles, and is connected with the evolution of stronger adhesion in edrioasteroids.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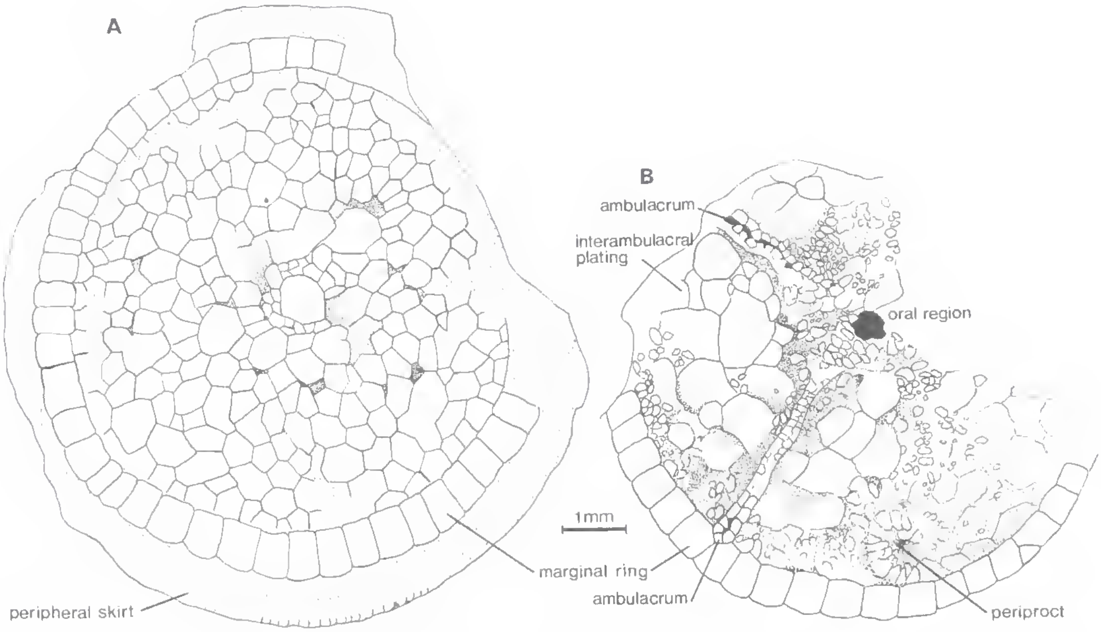


FIG. 12. *Edriodiscus primoticus* (Henderson & Shergold), QMF17856, camera lucida drawing of plating in a juvenile. A, aboral surface. B, oral surface. (see also Fig. 11C,D).

Edriodiscus Jell, Burrett & Banks, 1985

TYPE SPECIES

Cyclocystoides primotica Henderson & Shergold, 1971, by original designation.

AGE AND DISTRIBUTION

Early Middle Cambrian of Queensland.

DIAGNOSIS

Disc-like edrioasteroids with a ring of more than 40 marginal ossicles which are an integral part of both oral and aboral plated surfaces. Ambulacra extending over the marginal ossicles onto the peripheral rim.

REMARKS

This genus resembles *Cambraster* in having a well-developed marginal ring and ambulacra that extend onto and over this ring. Unlike *Cambraster*, however, it has a great many more marginal ossicles in the ring and these are tesselated into the aboral plated surface. In *Cambraster* marginal ossicles overlie the aboral plated surface and are not visible from beneath. Furthermore, the flooring plates of *Edriodiscus* are imperforate and the oral area resembles that of *Stromatocystites* more than *Cambraster*. In particular we have seen no evidence of there being a mouth frame of five large interradially positioned ambulacrals, which always appears prominently in *Cambraster* (Smith, 1986).

Jell *et al.* (1985) had only a single incomplete oral surface when establishing this genus. Further collecting has produced an additional five specimens, two of which show oral surfaces.

Edriodiscus primoticus (Henderson & Shergold, 1971)

Figs 11-14

Cyclocystoides primotica Henderson & Shergold, 1971, p. 706, pl.138, figs 1-3.

FIG. 11. *Edriodiscus primoticus* (Henderson & Shergold), early Middle Cambrian from QP243 near Cornford Bore. A,B, QMF17855a. A, general view of oral surface, x5. Note that much of the oral interambulacral plating has been lost to reveal the internal surface of aboral plates (see Fig. 13). B, enlargement of one ambulacrum to show the region of adradial plate alignment perpendicular to the ambulacral groove, x10. C,D, QMF17856, juvenile. C, aboral surface, x7. D, oral surface, x8. (see also Fig. 12). Latex casts whitened with ammonium chloride sublimate.

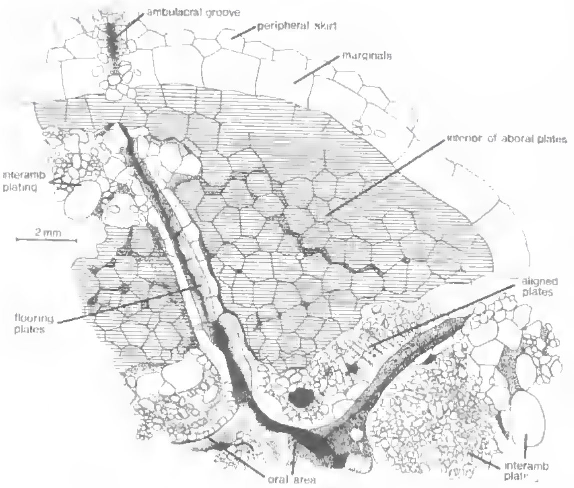


FIG. 13. *Edriodiscus primoticus* (Henderson & Shergold), QMF17855a, camera lucida drawing of oral surface. Much of the interambulacral plating has been lost to reveal the internal surface of aboral plates (horizontal lines).

'Cyclocystoides' primotica Henderson & Shergold: Smith & Paul, 1982, p. 677.

Edriodiscus primotica (Henderson & Shergold); Jell *et al.*, 1985, p. 190, figs 7a-c, 8.

Edriodiscus primotica (Henderson & Shergold): Smith, 1986, p. 753, fig. 20.

MATERIAL

Holotype CPC11395; paratype CPC11396; other material NMVP107479, QMF17855-7, BMNH E63525,63526.

AGE AND OCCURRENCE

From chert beds of the Yelvertoft Member, Beetle Creek Formation, early Middle Cambrian, exposed at locality QP243 (=NMVPL1598) 400-800 m south of the bore at Yaringa Creek, 50 km west-southwest of Mount Isa, western Queensland (GR 980965).

DIAGNOSIS

As for genus.

DESCRIPTION

Individuals 9-35 mm in diameter. All are circular in outline. The smallest has c. 55 marginal ossicles in the ring. These are differentiated from other plates and are longer (radially) than broad (Figs 11C,D, 12). Larger individuals have a similar number of marginal ossicles (50-60) but these are wider than long. At all sizes the marginal ossicles are an integral part of the aboral plated surface. Oral plating attaches to a weak ridge at the upper edge of the inner face of the marginals so that much of the inner face of the marginals must have been internal. The peripheral skirt is proportionally larger in small individuals but contains approximately the same number of plate rows at all sizes examined. At 9 mm diameter 4 irregular rows of plates make up the peripheral skirt, while at 15-35 mm diameter there are 4 or 5.

Ambulacra are straight and meet centrally in a 2:1:2 pattern (no specimen shows all five ambulacra but the best oral areas (Figs 11A, 13, 14) show two lateral ambulacra converging into a single ambulacral groove leading to ambulacrum III). Plating in this region shows no organization (Fig.14), suggesting that the cover plate sheet may have formed a permanent roof to the mouth. The ambulacra are straight and extend onto the marginal ring, where they overlie the marginal ossicles at a suture. In the smallest individual (9 mm diameter) the tip of the ambulacrum does not reach the outer margin of the marginal ring (Figs 11D, 12B) whereas in the largest the ambulacrum completely covers the marginals extending beyond to the edge of the peripheral skirt (Figs 11A, 13). No other oral plating extends beyond the marginal ring as far as we can tell. Ambulacral flooring plates are biserial and steeply inclined forming a deep, narrow groove. They are about 0.5 mm broad and a small part is exposed adradially. Sutural pores are not evident along the walls of the ambulacral groove (Fig. 13). Cover plates are small and multiple, except possibly towards the ambulacral tips in the smallest individual where there appear to be only primary cover plates (Figs 11D, 12B). A multiplated skirt of cover plates roofs the ambulacra close to the oral area. The structure of the oral frame remains unknown but the oral area is similar to that of *S. reduncus* (cf. Figs 11A, 13 with Figs 2A, 3).

Interambulacra are composed of large plates that are oval or subrounded in outline. Interspersed amongst these are smaller platelets of various sizes. There are no epispires or sutural gaps in the interambulacra (Fig. 11A,D). Platelets form an outer band close to the marginal ring and are also developed to the exclusion of larger plates close to the oral area (Figs 11A, 13). In the largest specimen the platelets close to the ambulacra are rod-like and preferentially aligned perpendicular to the ambulacral groove (Figs 11B, 13). Elsewhere platelets are randomly ar-

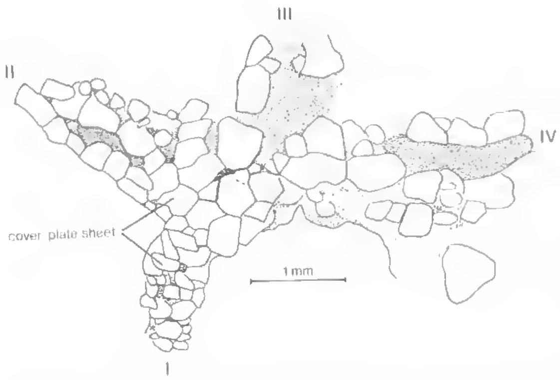


FIG. 14. *Edriodiscus primoticus* (Henderson & Shergold), NMVP107478, camera lucida drawing of plating in the oral region. Note the apparently disorganised arrangement of cover plates.

ranged. In juveniles (9 mm diameter) large plates dominate the interambulacral regions with little development of platelets (Figs 11D, 12B). This suggests that the large plates are laid down initially and that, during growth, areas of platelets developed preferentially around their interambulacral margins.

The aboral surface is a tesselate pavement of thick plates. In the smallest individual (Figs 11C, 12A) a large central plate is surrounded by a narrow ring of platelets. No circlets of plates can be recognized outside this region. The interior of the aboral surface is smooth and also forms a tesselate pavement (Figs 11A, 13). There is no sign of internal ribbing, as seen in *Stromatocystites* or *Totiglobus*, or of a central thickened platform.

REMARKS

This species was established for two specimens, both showing aboral surfaces. Henderson & Shergold (1971) interpreted this species as a cyclocystoid, but Smith & Paul (1982) later removed it from the cyclocystoids, interpreting it as a probable edrioasteroid. This was confirmed by Jell et al. (1985) when they discovered and described a third example showing part of the oral surface. Further collecting by the authors has yielded 5 more specimens, 3 of which are part and counterpart, showing details of both surfaces. The above description supplements those given previously.

Alignment of rod-like interambulacral plates bordering the ambulacra is noteworthy because of its resemblance to the arrangement of virgals in *Archegonaster*.

Order ISOROPHIDA Bell, 1976

Previously edrioasteroids have been divided into three orders, Stromatocystitida, Isorophida and Edrioasterida (Bell,1980). Stromatocystitids have a fully plated theca, biserial ambulacra, flooring plates with sutural pores, and interambulacral plates with epispires. Isorophids have an uncalcified aboral surface, a differentiated peripheral ring and uniserial flooring plates, while edrioasterids have biserial flooring plates with an exposed adradial portion, no differentiated peripheral ring and a partially or completely calcified aboral surface. A fourth group, the Cyathocystida was recently erected to accommodate turret-shaped edrioasteroids with single large 'deltoid-like' flooring plates (Bockelie & Paul, 1983). Smith (1986) modified this scheme somewhat by rejecting the Stromatocystitida as a paraphyletic ancestral group. The two Upper Cambrian edrioasteroid genera described below show mixed characteristics and appear to bridge the gap between Lower and Middle Cambrian stromatocystitids and the Ordovician and later isorophids. Synapomorphies shared with later isorophids include the disc-like body form, the imbricate plated peripheral rim, the form of the hydropore, the absence of aboral plating and the presence of simple cover plates rather than a cover plate sheet. Because of these features they are best regarded as primitive isorophids. However both *Hadrodiscus* and *Chatsworthia* may have biserial flooring plates and the former has an oral frame of five interradially positioned deltoid plates of ambulacral origin. Neither have the typical uniserial flooring plates of Ordovician isorophids as far as we can tell.

The uniserial flooring plates of later Isorophida could have arisen in one of three ways. Firstly, each uniserial flooring plate could be the result of fusion of opposite pairs of originally biserial flooring plates. Secondly each uniserial flooring plate could have originated from a single biserial flooring plate by extending the amplitude of the V-shaped perradial suture until it reached the opposite edge, (the reverse of the suggested derivation of biserial from uniserial arm plating in crinoids - viz. Bather, 1900). Finally the uniserial flooring plates could represent a new structure not homologous with biserial flooring plates. The Upper Cambrian species described below show no evidence of extended V-shaped perradial sutures, having almost straight perradial sutures instead. Furthermore, the second hypothesis would require a secondary series of primary cover plates and cover plate articulations to develop. No evidence exists to suggest that this might have been the case, in contrast, for example, to the situation with uniserial crinoid arms, where sequential uniserial arm plates carry cover plates on alternate sides.

Of the two genera described below *Hadrodiscus* appears, tentatively, to be the more primitive, having a poorly differentiated peripheral rim and small, closely fitting pentagonal cover plates. Flooring plate arrangement is inadequately known but may have been biserial. In *Chatsworthia* the peripheral rim plating is much better differentiated, as in most later isorophids, and there is a system of stout, spine-like cover plates that are non-contiguous when held erect. A similar cover plate arrangement is found in early lebetodiscids such as *Foerstediscus* for example. However, in *Chatsworthia* the relationship of cover plates to flooring plates is still unclear. Either cover plates are firmly sutured on to the flooring plates so that both generally act as a single ossicle, or the primary cover plates of later isorophids are in fact modified flooring plates that have taken on the role of protecting the radial water vessel. In either case, it would appear that the uniserial flooring plates in more derived isorophids represent a new system of plates independent of the biserial flooring plates of other edrioasteroids.

Hadrodiscus gen. nov.

ETYMOLOGY

Greek *hadros*, elegant or delicate.

TYPE SPECIES

Hadrodiscus parma sp. nov.

AGE AND DISTRIBUTION

Median Upper Cambrian (Franconian) of western Queensland, Australia.

DIAGNOSIS

An isorophid with a poorly differentiated peripheral ring, straight ambulacra with small, tightly fitting cover plates and larger oral cover plates. Hydropore/gonopore a large, prominent opening. Oral frame composed largely of stout, wing-shaped elements.

REMARKS

The taxonomic position of *Hadrodiscus* remains problematic largely because it is incompletely known. Although the ambulacra are floored we do not yet know what the plate arrangement is. The relatively small size of the cover plates seen externally and the suggestion of large, possibly biserially arranged plates forming the floor of the ambulacral grooves suggest to us that *Hadrodiscus* had both cover plates and flooring plates, as in *Stromatocystites*. However, the presence of a peripheral rim, the complete absence of aboral plating, the position and form of the hydropore opening and the large oral frame plates that are interradial in position and are undoubted flooring plates, mark *Hadrodiscus* as more advanced than *Stromatocystites*. It is less derived than *Chatsworthia* which has a system of large biserially arranged cover/flooring plates and a better differentiated peripheral rim. At present we consider it to be the most primitive known isorophid.

Hadrodiscus parma sp. nov.

Figs 15-18, 20C

ETYMOLOGY

Greek *parme*, a small shield, in allusion to its appearance.

MATERIAL

Holotype QMF17874; paratypes QMF17875, BMNH E63527.

AGE AND OCCURRENCE

All specimens come from locality K204 of Shergold (1982), from a grey, 4 m thick, limestone unit of the Chatsworth Limestone, 3.5 km south of Chatsworth homestead, 60 km southeast of Duchess, western Queensland, *Peichiashania secunda-Prochuangia glabella* Assemblage Zone, median Upper Cambrian (Franconian).

DIAGNOSIS

A *Hadrodiscus* with about 10-12 primary cover plates in a column at disc diameters of 6-7 mm, these primary cover plates being small, squarish and close-fitting. Peripheral rim composed of 4 or 5 irregular rows of small imbricate plates not clearly differentiated from interambulacral areas.

DESCRIPTION

Specimens are circular in plan view and flattened hemisperical in profile. In diameter the holotype is c. 7 mm (Figs 15A, 16) and the two other specimens c. 6 mm (Figs 15B,C, 20C). The

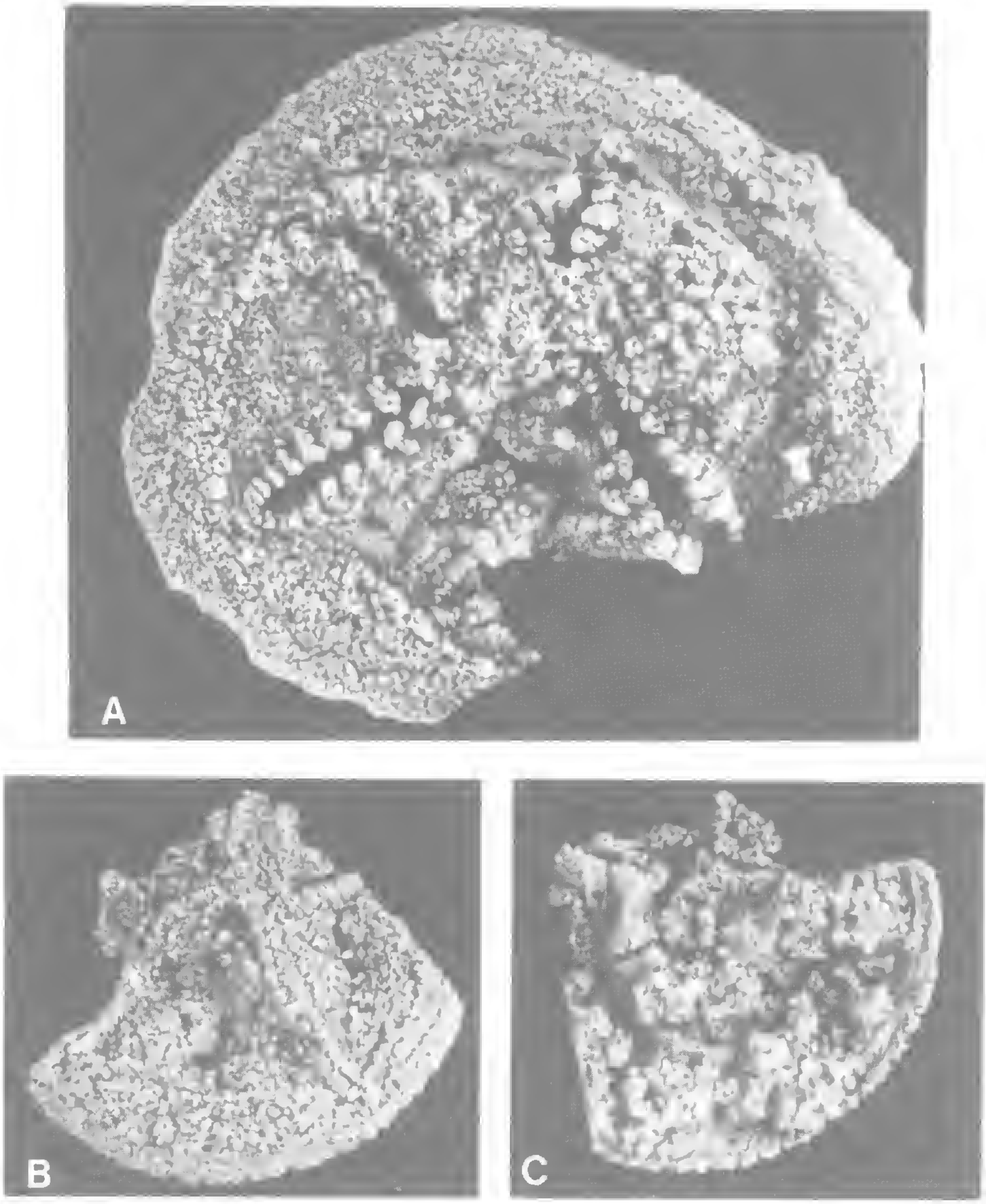


FIG. 15. *Hadrodiscus parma* sp. nov., from the Chatsworth Limestone, median Upper Cambrian of Chatsworth. A, QMF17874, holotype, oral surface, x12 (see also Fig. 16). B,C, BMNH E63527, paratype. B, external oral surface, x10. C, internal view of same, x10 (see also Fig. 18). Silica replacements coated with ammonium chloride sublimate.

aboral surface is uncalcified and the peripheral rim of the disc flares outwards. There has been no post-mortem collapse of the disc relative to the peripheral rim so that the boundary between the two regions is not well demarcated, there being virtually a smooth transition from rim to centre. The oral area forms the summit of the disc and is centrally positioned. Specimens appear to be unattached to any substratum.

The peripheral rim is composed of 4 or 5 irregular rows of small imbricate plates, 3 or 4 abreast in one interambulacral segment (Figs 15A, 16). These plates overlap towards the centre on their outer face, and have convex proximal edges. However, sutures are weakly defined suggesting that the plate boundaries, though imbricate, were almost flush and that the plates themselves did not override more proximal plates to any extent. The same is true of the inner face where no plate boundaries can be made out at all. None of the marginal plates is geniculate or has a thickened aboral edge. Instead the peripheral rim remains uniformly thin and only the base of the rim would have contacted the substratum. Plates in the rim are similar in size except towards the periphery where the outermost plates are much smaller. The boundary between peripheral rim plating and the interam-

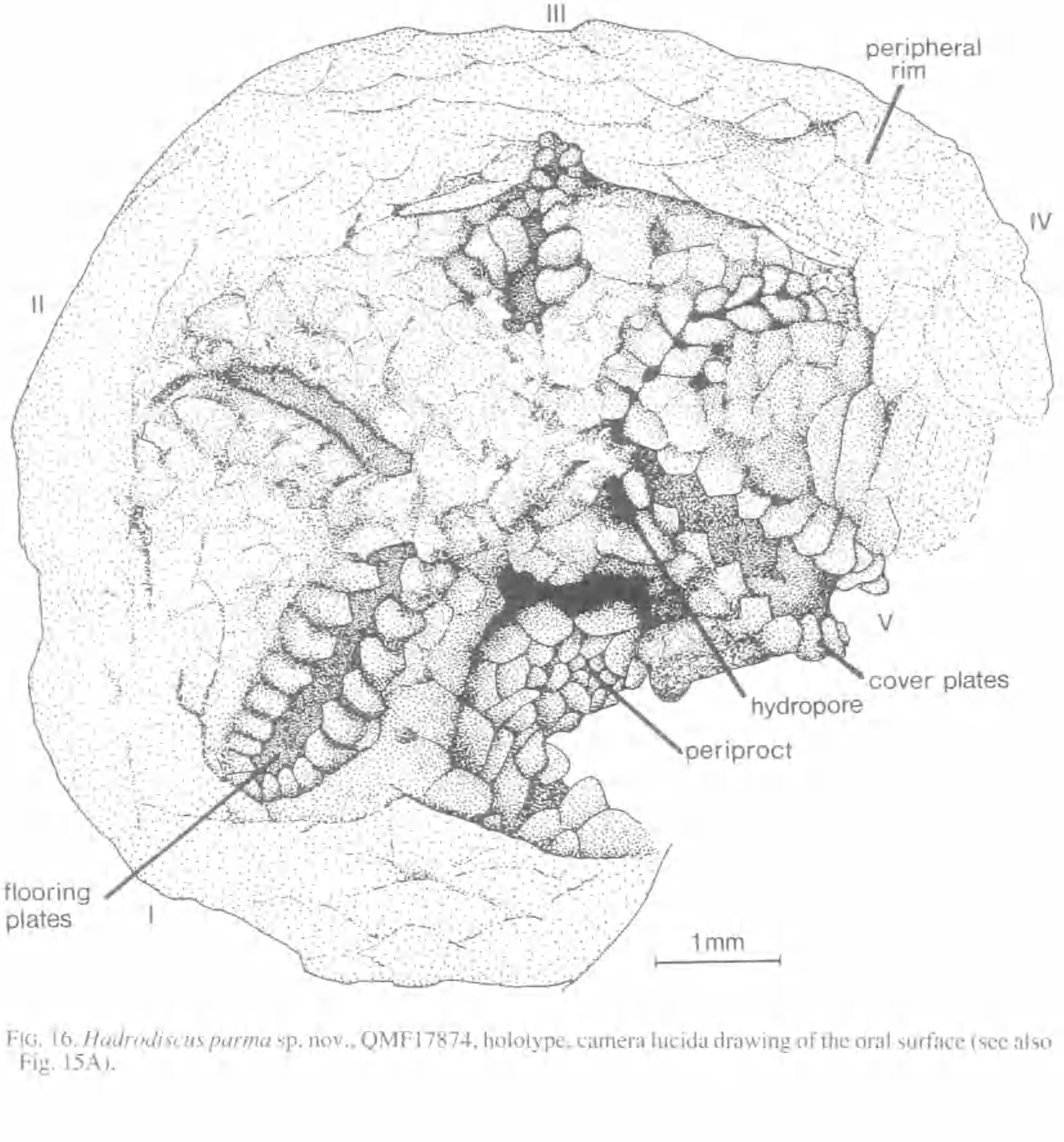


FIG. 16. *Hadrodiscus parma* sp. nov., QMF17874, holotype, camera lucida drawing of the oral surface (see also Fig. 15A).

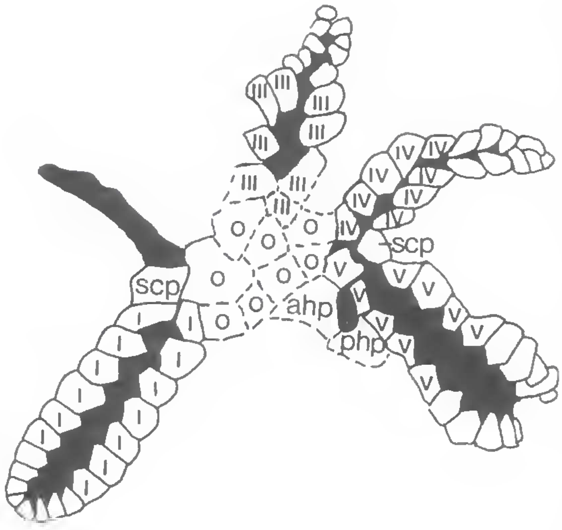


FIG. 17. *Hadrodiscus parma* sp. nov., QMF17874, holotype, interpretation of cover plate arrangement. I-V = cover plates of ambulacra I - V; o = shared oral cover plates; ahp = anterior hydropore plate; php = posterior hydropore plate; scp = shared cover plate.

bulacral plates of the disc is not marked, interambulacral plating appearing to merge gradually into that of the peripheral rim, except in the posterior interambulacrum. Again, plate boundaries here are probably subtesselate as none stand out clearly (Figs 15A,B, 20C).

The ambulacra are relatively long and reach about 80% of the radius to the edge. They indent the peripheral rim plating to a small extent (Figs 15A, 16). In the holotype, ambulacra I, III and V are straight, or virtually so, while ambulacrum II curves clockwise and ambulacrum IV curves anticlockwise (Figs 15A, 16). However, this is probably a post-mortem artefact since the disc has collapsed towards the anterior, and the 3 adjacent ambulacra (probably I, II and III) in one of the paratypes (Fig. 20C) are straight. The ambulacra are parallel-sided and have rounded, blunt tips (Figs 15A,B, 20C). In the holotype cover plates are present in all ambulacra except II, where they have been lost (Fig. 16). In ambulacra I and V the cover plates are in the open position, in ambulacra IV they are in the closed position, while in ambulacrum III they are largely disrupted from life position. Cover plates were able to open widely along the length of the arm but probably formed a permanent cover to the oral area, as no clear perradial suture is apparent in this region (Fig. 15A,B). There are about 10-12 primary cover plates in a column at this diameter. The primary cover plates abut along most of their length and end in a V-shaped edge which may be hooked towards the oral region (Figs 15A, 16, 20C). Cover plates on either side of the ambulacrum alternate to interlock, although those seen in ambulacrum IV of the holotype are almost opposite due to distortion of the disc. Sutural gaps between adjacent cover plates are not apparent.

Ambulacral grooves are moderately deep with a smooth rounded floor. Sutures are not visible suggesting that flooring plates were probably solid and robust although this appearance may be due to their coarse silicification. No part of the flooring plates can be seen along the adradial margin of the ambulacra and it would appear that the interambulacral plating abuts against the outer edge of the cover plates. In ambulacrum II of the holotype cover plates have been lost revealing the ambulacral groove (Figs 15A, 16). Upper edges of flooring plates define the walls of this groove but again the detailed structure has been lost in silicification.

The internal surface of one specimen (Fig. 15B,C) reveals the 5 ambulacral grooves. Around the mouth these are floored by large deltoid-shaped plates lying interradially and forming the mouth frame (Figs 15C, 18). Elsewhere ambulacral grooves are partially open (possibly due to incomplete silicification) although larger plates adjoin the ambulacral groove and may have floored the groove in life. If these plates are flooring plates then each plate must have carried 2-4 of the cover plates.

In external view the oral area is best seen in the holotype (Figs 15A, 16) where the cover plates form an unbroken roof to the mouth. Plate sutures are nowhere clear and our interpretation of oral plating is highly tentative. The hydropore, however, is distinct as a deep depression in the posterior interambulacrum close to ambulacrum V (Figs 15A, 16). It has a narrow, bar-like ambulacral cover plate on its adradial margin and 2 moderately large plates forming the posterior border. These posterior plates lie well below the ambulacra and would appear to be modified ambulacral flooring plates that have been enlarged into the posterior interambulacrum to incorporate the hydropore/gonopore. The remainder of the oral area consists of a number of small plates, to judge from the surface irregularities preserved. Left and right branching plates are easily identified but the plating in the

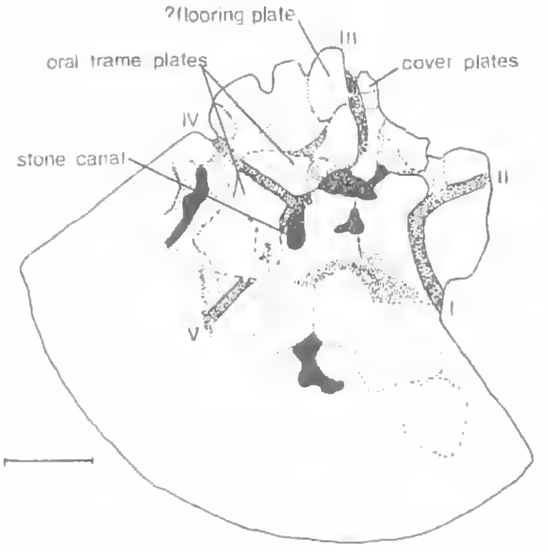


FIG. 18. *Hadrodiscus parma* sp. nov., BMNH E63527, paratype, camera lucida diagram of interior of oral surface showing the mouth frame plates and arrangement of the water vascular system. Scale bar = 1 mm.

posterior part is less clear. A continuous row of small, squarish cover plates may form the posterior edge of the oral area and connect the cover plate series of ambulacra I and V (Fig. 16). Conversely, this may be a single laterally elongate posterior oral plate that is slightly fractured. Other plates lie anterior of this but no enlarged anterior oral plates are clearly differentiated.

The interior of the oral surface (Figs 15C, 18) shows the 5 ambulacral channels around a central mouth. A sixth groove originates close to the base of ambulacrum V and rapidly curves towards the outer surface; this is the hydropore groove and terminates externally at the hydropore. At the angle between ambulacra IV and V is a large deltoidal plate. This has a median saddle and may be composed of 2 plates tightly sutured together, but the coarseness of the silicification prevents us from deciding whether this is indeed a single plate. In the posterior interray there appear to be 2 large polygonal plates, the plate closer to ambulacrum I having a prominent adoral projection. Other mouth frame plates are not evident and are presumably lost (possibly during etching).

Interambulacral plating consists of a small number of apparently subtesselate plates (Figs 15A, 16). These have curved adoral plate boundaries close to the peripheral rim but become more polygonal in outline towards the centre. Only traces of sutures are seen in both specimens.

A large periproct occupying most of the posterior interambulacrum (Figs 15A,B, 16) consists of a mound-like region of imbricate plates which become progressively smaller towards the centre. The middle of the periproct consists entirely of small platelets.

REMARKS

This species is readily distinguished from the contemporary *Chatsworthia spinosa* by its smaller, more tightly fitting and more numerous primary cover plates, its more numerous and smaller peripheral rim plates and more robust suturing between peripheral rim and interambulacra. In all specimens of *C. spinosa* the disc has collapsed well below the level of the peripheral rim and presumably marks a weak point. The marked difference in appearance of the primary cover plates between *C. spinosa* and *H. parma* makes it most unlikely that the two forms simply represent different states of preservation of the same species (cf. Fig. 20A,B with Fig. 20C).

The distinct groove leading from the circumoesophageal ring of the water vascular system and opening close to the base of ambulacrum V in the posterior interray proves that this opening is a hydropore. Smiley (1988) speculated that primitive echinoderms might have internal hydropore openings and that the opening generally referred to as the hydropore might represent the gonopore.

Chatsworthia gen. nov.

ETYMOLOGY

For Chatsworth Station, on which the specimens were discovered.

TYPE SPECIES

Chatsworthia spinosa sp. nov.

AGE AND DISTRIBUTION

Median Upper Cambrian (Franconian) of Queensland, Australia.

DIAGNOSIS

An isorophid with short, virtually straight ambulacra and undifferentiated oral cover plates. Cover plates stout and erect, forming a single alternating biseries; well separated when open.

Biserial arrangement of flooring plates meeting perradially to floor the ambulacral groove.

REMARKS

This genus is distinguished from *Hadrodiscus* in the size and spacing of primary cover plates and plating of the peripheral rim and in the structure of the oral frame and flooring plates. In *C. spinosa* there are only 6 or so primary cover plates in each ambulacrum and the peripheral rim is composed of a small number (usually 10) of large plates with just 2 rows of small, outer platelets. In *Hadrodiscus parma* the primary cover plates are more slender and closely spaced, with about 12 in a row at an equivalent disc diameter, and the peripheral ring is composed of a greater number of relatively smaller imbricate plates. *C. spinosa* is not sufficiently well preserved for the structure of the ambulacra to be determined unambiguously, but it appears to consist of a biseries of plates that meet perradially to floor the ambulacral groove. Above and possibly continuous with these are stout, spine-like, cover plates, undoubtedly homologous to the primary cover plates of later isorophids.

Chatsworthia spinosa sp. nov.
(Figs 19, 20A,B, 21-28)

Isorophid indet. Jell, Burrett & Banks, 1985, p.195, fig. 9.

ETYMOLOGY

Latin *spinosus*, thorny, referring to its cover plate series.

MATERIAL

Holotype QMF17944; paratypes QMF 17945-51, NMVP107129, 108990, BMNH E63528-30. Other material QMF17952-9, BMNH E63531.

AGE AND OCCURRENCE

All specimens come from locality K204 of Shergold (1982), from a grey, 4 m thick, limestone unit of the Chatsworth Limestone, 3.5 km south of Chatsworth homestead, 60 km southeast of Duchess, western Queensland. *Peichiashania secunda-Prochuangia glabella* Assemblage Zone, median Upper Cambrian (Franconian).

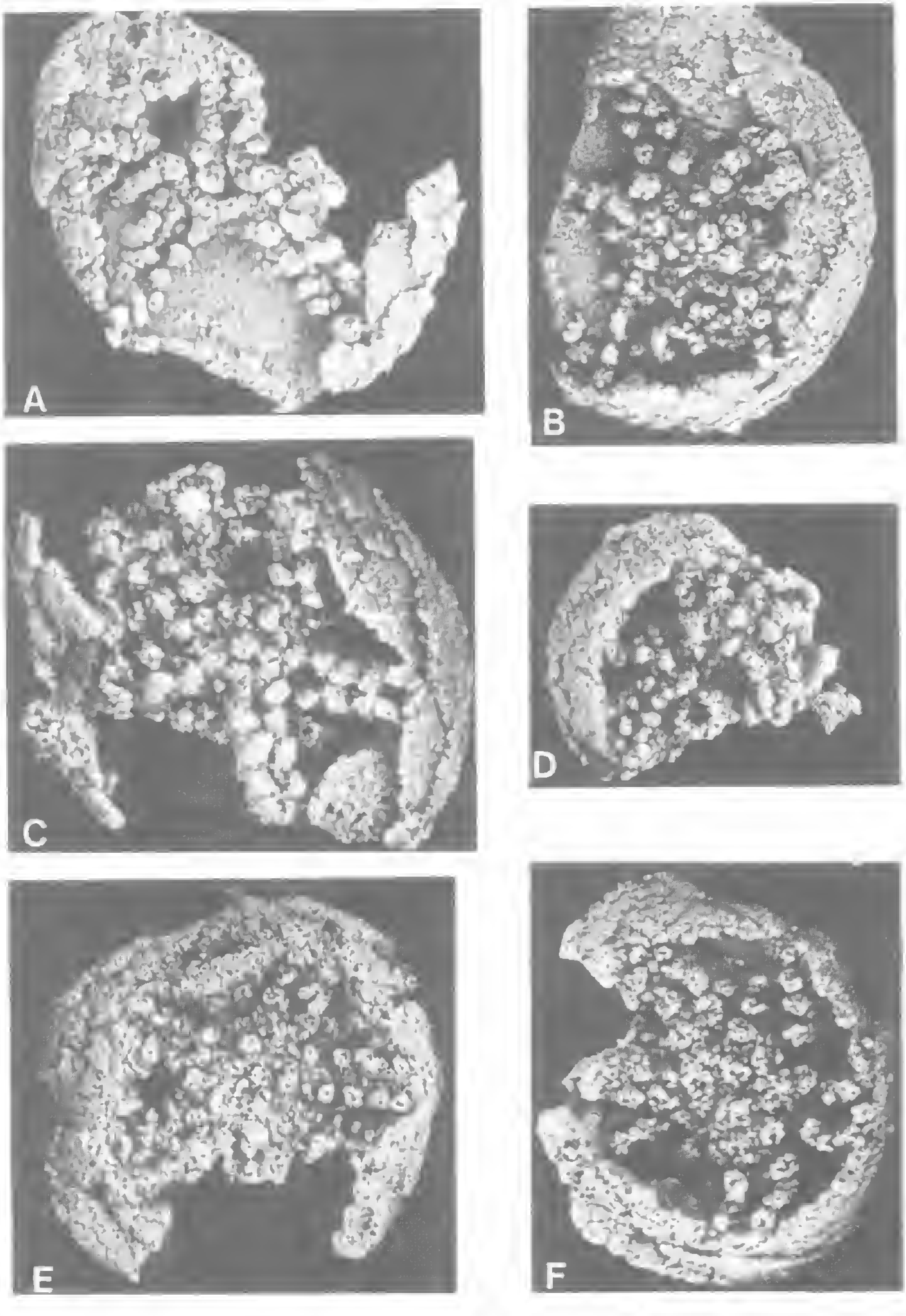
DIAGNOSIS

A *Chatsworthia* with 5 or 6 stout, spine-like cover plates in each ambulacrum and a peripheral rim composed of *c.* 10 large plates plus smaller accessory plates distally.

DESCRIPTION

Theca circular in outline with a diameter of 6-10 mm. The peripheral rim is well developed and differentiated from the disc, which in all specimens has collapsed slightly beneath the level of the rim (Fig. 19). The theca has a low profile, though in life the disc may have been low domed. Only the oral surface is heavily plated. The aboral surface, where seen, shows no evidence of having had large plates. However, the surface always appears granular (Fig. 26) and there remains the possibility of a calcified lower surface of tiny granules. The peripheral rim is relatively broad, forming up to half the radius of the theca interradially, and indented radially for the ambulacra (Figs 19B, 21). In profile the rim slopes steeply outwards at about 40°. The rim is usually composed of 5 large radial and 5 large interradial plates which alternate and overlap one another (Figs 21, 25), but the arrangement is not strict and there may be an extra plate in one or other of the interambulacral regions. Peripheral rim plates have curved outer edges and are differentiated from interambulacral plates of the disc. On the distal part of the rim there are two irregular rows of smaller plates, the outermost series being the smallest (Fig. 27A). These also appear to imbricate, although plate sutures are rarely well marked. These plates may completely overlie the 10 larger plates and are commonly lost. When viewed from the interior the peripheral rim appears smooth and no plate boundaries can be identified. This would suggest that the plates are subtesselate and firmly bound together along sutures and explains why the peripheral rim is generally preserved in an uncollapsed state. Peripheral rim plates are neither geniculate nor expand into a flattened base. Thus the rim has a uniform thickness and only the bottom of the rim would be in contact with the substratum.

Ambulacra are straight, rather short, and broad. They extend to the peripheral rim which they indent but do not overlap (Figs 19, 20A,B). The 4 to 6 large, spine-like cover plates in each ambulacral column (Figs 21-25) have a broad base and taper distally (Fig. 27B,C) and in some cases tips of the cover plates appear to be curved towards the centre of the disc. Cover plates may be preserved in the closed position with the ambulacra appearing as tall, rather narrow ridges


A
B
C
D
E
F

(Fig. 19A,C). In such cases cover plates are inclined towards the centre and overlap their neighbours forming a canopy to the ambulacral channel. They alternate across the perradius. More often specimens are preserved with the ambulacra open and cover plates erect and form-

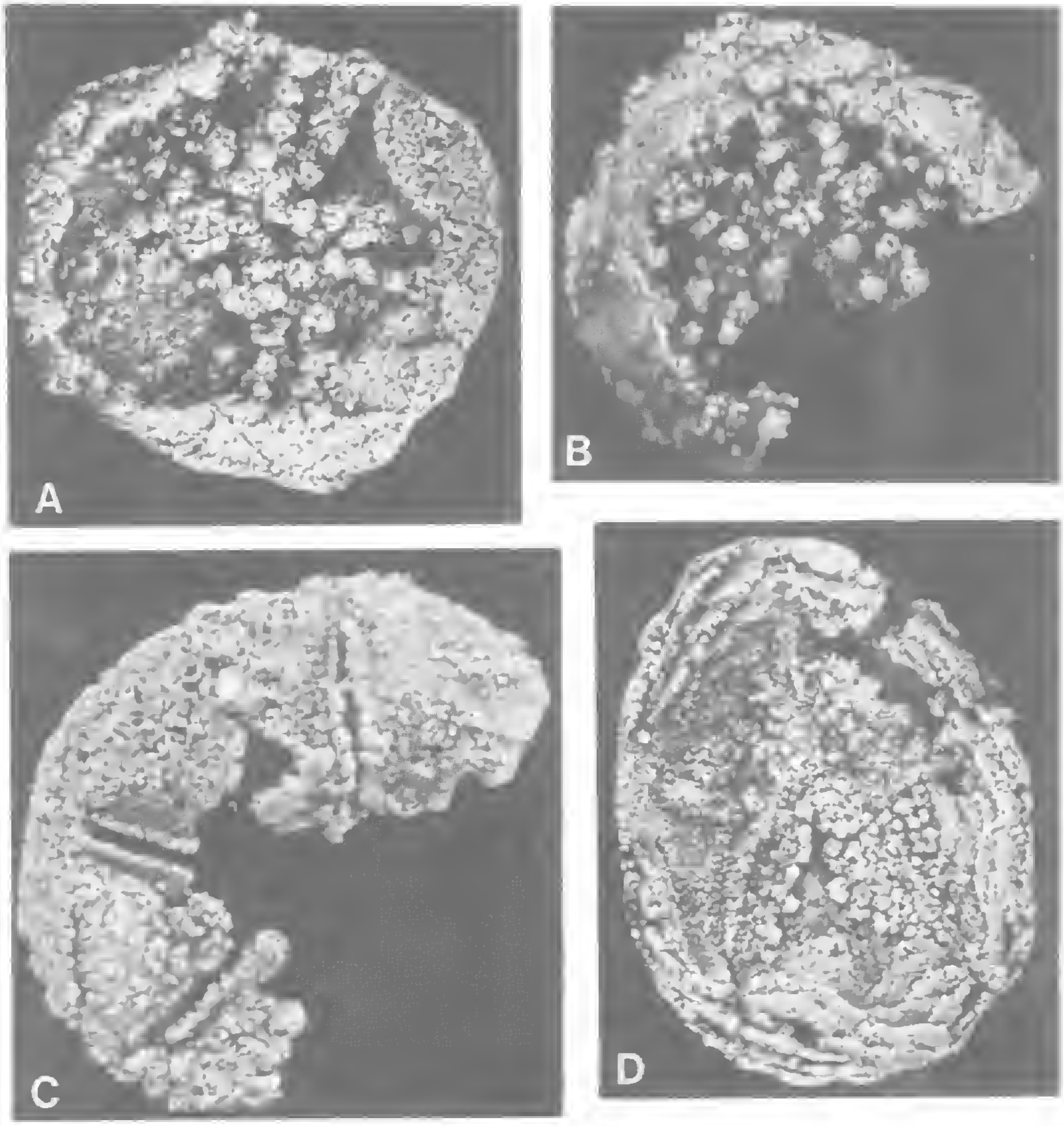


FIG. 20. A,B,D. *Chatsworthia spinosa* sp. nov. A, QMF 17949, paratype, x7. B, NMVP108990, paratype, x6. C, *Hadrodiscus parma* sp. nov., QMF17875, paratype, x12. D, ?*Hadrodiscus* sp. QMF17943, internal surface, x7. Silica replacements from the Chatsworth Limestone, median Upper Cambrian, of Chatsworth, whitened with ammonium chloride sublimate.

FIG. 19. *Chatsworthia spinosa* sp. nov., from the Chatsworth Limestone, median Upper Cambrian of Chatsworth. A, BMNH E63528, paratype, x8 (see also Fig. 22). B, QMF17944, holotype, x7 (see also Fig. 21). C, NMVP107129, paratype, x6.5 (see also Fig. 23). D, QMF17948, paratype, x8 (see also Fig. 25). E, QMF17945, paratype, x7. F, QMF17947, paratype, x9. Silica replacements coated with ammonium chloride sublimate.

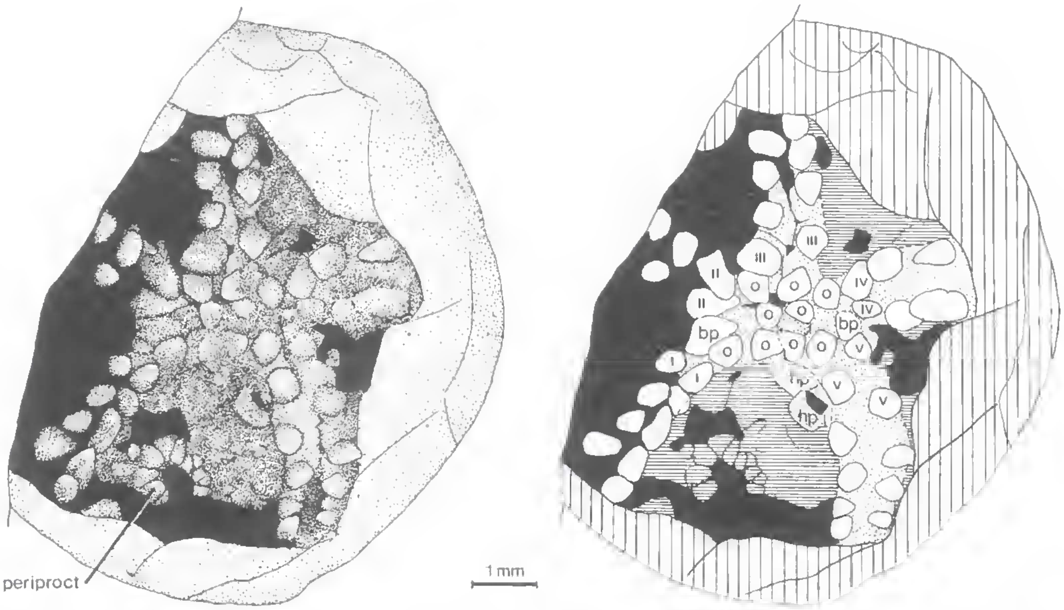


FIG. 21. *Chatsworthia spinosa* sp. nov., QMF17944, holotype, camera lucida drawing and plate interpretation diagram. Vertical hatching = peripheral rim plating; horizontal close hatching = interambulacral plating; stippling = ambulacral zones undifferentiated; blank = cover plates; black = missing. Ambulacral cover plates are labelled as follows: I-V = cover plates of ambulacra I - V, bp = lateral branch plate, o = shared oral plate, hp = hydropore plate.

ing a border to the food groove (Figs 19B,E,F, 20B). In such cases the cover plates are well separated leaving broad gaps between. Spine-like cover plates are less well-developed over the oral area.

The ambulacral groove itself may be preserved in the open position, as a broad U-shaped channel, or in the closed position, as a narrow slit-like trench. This alone indicates that the ambulacrum is floored by a biseries and in cross-section, although a perradial suture cannot be identified due to the coarse nature of the silicification, a discontinuity of shape indicates where it probably lay (Fig. 27B). Furthermore, from the interior the perradial line appears as a sharp ridge and in one specimen (Fig.26) the interior of the ambulacra show possible biserial flooring plates. However, the arrangement of flooring plates is nowhere clearly seen, due to the coarse nature of the silicification, and the junction between cover and flooring plates remains problematic.

In the oral area, the spine-like plates become less evident and cover plates appear more plate-like. Coarse silicification again hinders interpretation of oral plating. The arrangement of plates is probably best seen in the holotype (Fig. 21) and two of the paratypes (Figs 22, 23). The ambulacra meet in a 2:1:2 pattern with small lateral branch plates at the inner angles of ambulacra I and II, and IV and V. No noticably enlarged oral plates are developed. A row of 4 cover plates forms the posterior part of the oral area, the outer 2 abutting the lateral branch plates. In BMNH E63528 (Fig. 22) only a single large plate occupies this region. This could represent an oral frame plate devoid of its two cover plates. The central 2 posterior plates lie opposite 2 anterior cover plates and roof the central part of the oral area. No secondary or accessory cover plates can be distinguished, but this could be due to poor preservation. The oral frame, if our interpretation is correct, is composed of 3 large flooring plates(Fig. 22), 2 anterior plates occupying the angles between ambulacra II and III and between III and IV, and a single broad posterior plate. It is not known whether there are also enlarged flooring plates between the lateral ambulacra that also contribute to the oral frame. The hydropore/ gonopore opens in the posterior interradius close to the base of ambulacrum V. There is a large U- shaped plate that forms the posterior and interradial border to the opening and a narrower plate forms its adoral border.

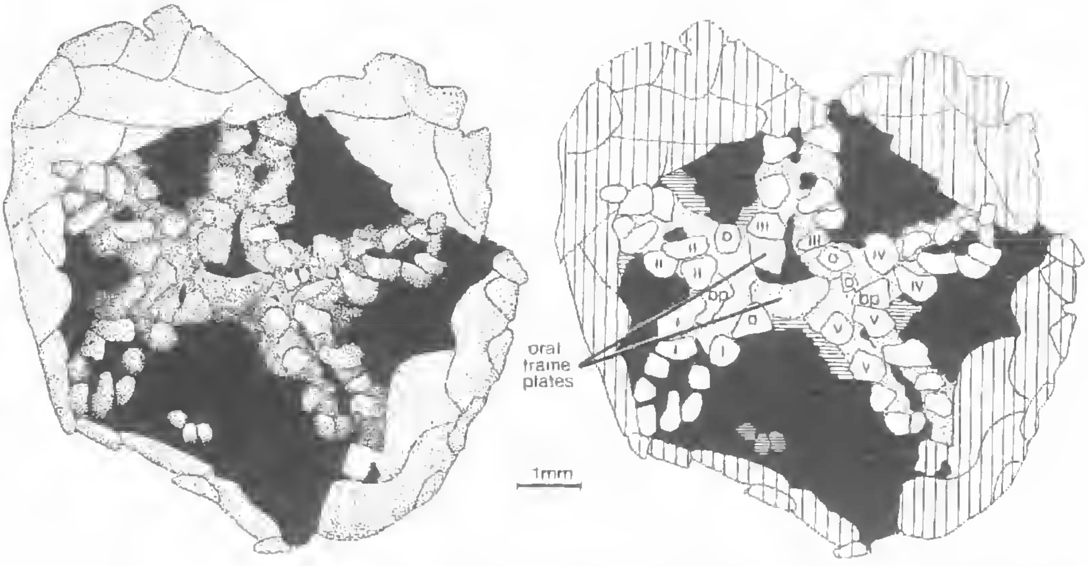


FIG. 22. *Chatsworthia spinosa* sp. nov., BMNH E63528, paratype, camera lucida drawing and plate interpretation diagram. Symbols as in Fig. 21.

Both have the position and appearance of being modified ambulacral flooring plates. When viewed from the interior (Fig. 26) the oral area stands out as a C-shaped ridge open towards the posterior. The ridge on the hydropore side lies more distal and creates a more open curve than the ridge on ambulacrum I. The posterior oral flooring plate must therefore have considerably less depth than the other oral frame plates.

Interambulacral areas are relatively small and wedge-shaped. No specimen shows undisrupted plating but small ovoid plates can be discerned in a number of specimens. There is no evidence of epispires between interambulacral plates which were presumably either imbricate or subtesselate. The periproct is a conical structure occupying much of the posterior interambulacrum (Figs 19, 21, 24, 25). About 8-10 wedge-shaped plates form the periproctal cone and possibly smaller granular plates occur at the summit.

REMARKS

This species was first illustrated and described by Jell *et al.* (1985) on the basis of 2 moderately well-preserved specimens from our type locality. They recognized it as an isorophid but, because certain key characteristics could not be identified from that material, it was left under open nomenclature. We have since collected a further 21 specimens and, although none is particularly well preserved, there is now sufficient material to establish the basic morphology of this species.

A major uncertainty remains as to whether there are separate covering and flooring plates, since once again no clear sutures can be made out. It is probable that the flooring plates form the U-shaped groove and the cover plates are the spine-like projections that arise from this. However, we have not seen any specimen in which clearly separated cover plates and flooring plates can be unambiguously distinguished, and it is therefore possible that only a single set of plates is present, acting as both flooring and cover plate, articulating perradially and carrying a long spinous projection. The similarity of the spine-like plates in *C. spinosa* to cover plates of other isorophids, such as *Foerstediscus*, is striking, and there can be little doubt that the plates seen in *Chatsworthia* are indeed homologous to those of other isorophids.

C. spinosa is distinguished from the co-occurring isorophid, *H. parma*, by its simpler and stouter peripheral rim and more robust ambulacral cover plates that are much fewer in number.

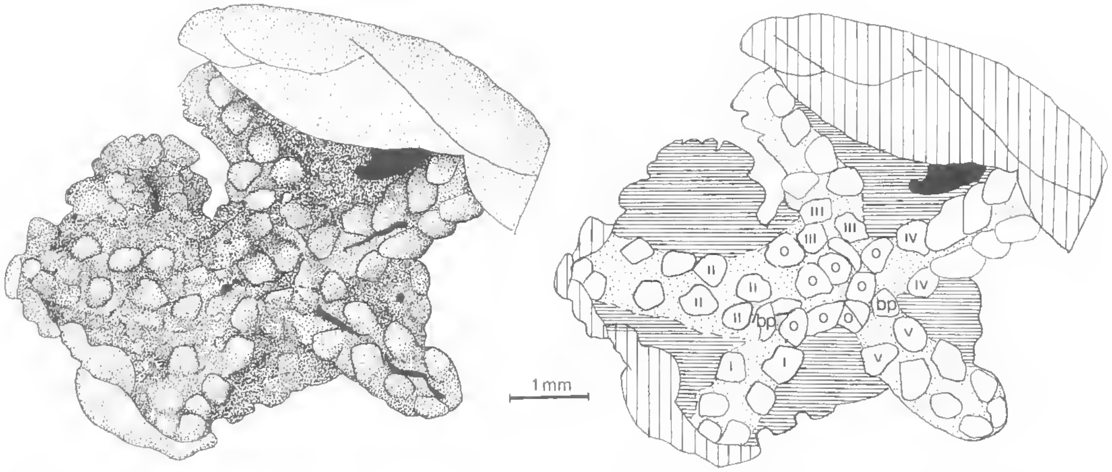


FIG. 23. *Chatsworthia spinosa* sp. nov., NMVP 107129, paratype, camera lucida drawing and plate interpretation. Symbols as in Fig. 21.

Order EDRIOBLASTOIDA Fay, 1962
Family ASTROCYSTITIDAE Bassler, 1938

TYPE GENUS

Astrocystites Whiteaves, 1897 [Type species: *Astrocystites ottawaensis* Whiteaves, 1897]; Trentonian (Caradocian, Ordovician) of Ottawa, Canada.

OTHER SPECIES

Astrocystites distans Webby from the Lower Caradocian of New South Wales [possibly a subjective junior synonym]: *Cambroblastus enubilatus* sp. nov. from the Franconian, Upper Cambrian of Queensland.

RANGE

Median Upper Cambrian to mid Ordovician.

DIAGNOSIS

Edrioasteroids with a polyplated stalk and a bud-shaped theca with 5 basals. Ambulacra prominent with primary cover plates only. Flooring plates exposed adradially, primitively biserial but may be reduced to a single mouth angle flooring plate situated at each interradial angle.

REMARKS

Edrioblastoids are probably the rarest of echinoderm groups that have been given class status. Although *Astrocystites ottawaensis* has been known since 1897 few specimens have ever

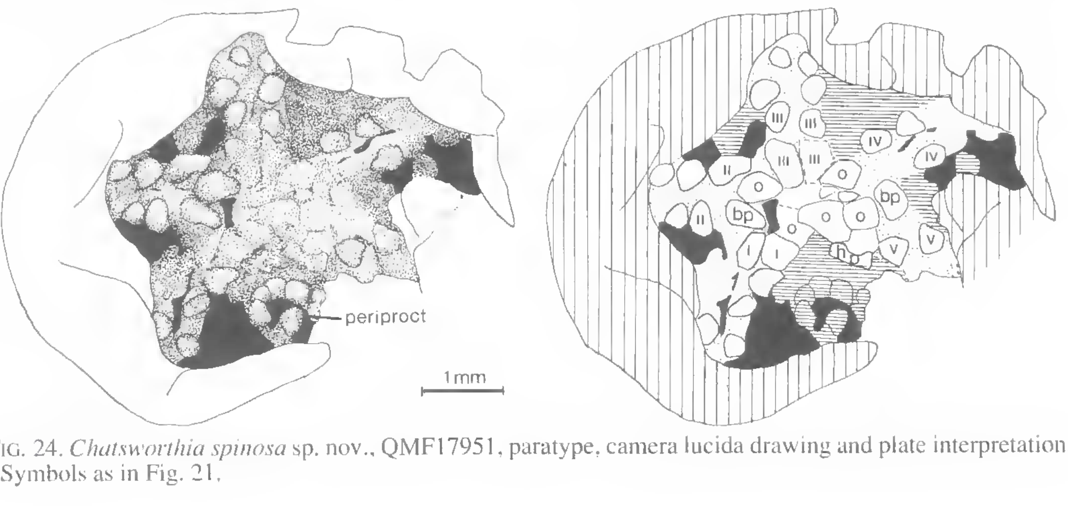


FIG. 24. *Chatsworthia spinosa* sp. nov., QMF17951, paratype, camera lucida drawing and plate interpretation. Symbols as in Fig. 21.

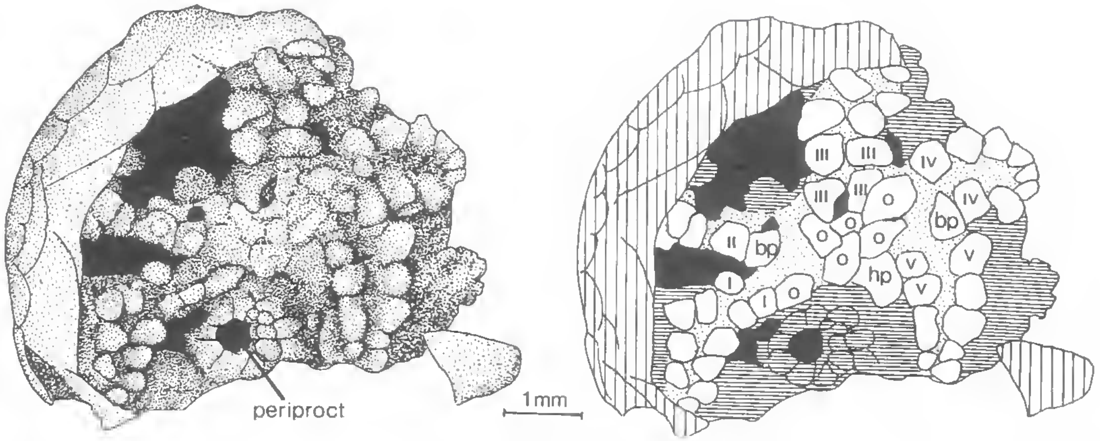


FIG. 25. *Chatsworthia spinosa* sp. nov., QMF17948, paratype, camera lucida drawing and plate interpretation. Symbols as in Fig. 21.

been collected. The species was erected on the basis of 3 specimens from the Trenton Limestone (Middle Caradocian) at Kirkfield Quarry, Ontario; 2 held in the Canadian Geological Survey collections of which one is the lectotype and the other is lost, and a third held in the British Museum (Natural History). Mintz (1970) described a fourth specimen from the type locality and horizon. A second species, *A. distans*, was described from the basal Caradocian Cliefden Caves Limestone of New South Wales (Webby, 1968) based on two tolerably complete specimens and a number of fragments. Mintz (1970) believed that *A. distans* was probably a subjective junior synonym of *A. ottawaensis*. Sprinkle (1982) described a small number of isolated deltoid plates of an edrioblastoid from the mid Ordovician Bromide Formation of U.S.A. and deltoid plates also occur in the Upper Ordovician Boda Limestone of Sweden (C.R.C. Paul, pers. comm. November, 1989).

Ordovician edrioblastoids have a highly distinctive morphology and have been difficult to relate to other echinoderm groups. When they were originally described they were thought to be most closely related to the diploporite cystoid *Asteroblastus* (Whiteaves, 1897). Bather (1900, 1914) redescribed the material then available and placed the species in its own family within the edrioasteroids. Hudson (1925, 1927), however, argued for their close association with blastoids as did Fay (1962, 1967), while both Webby (1968) and Bell (1980) have related them to edrioasteroids and Mintz (1970) to eocrinoids. Paul (1988) commented that *Astrocystites* was so unusual in its morphology that it could not be placed in his phylogenetic scheme of cystoids.

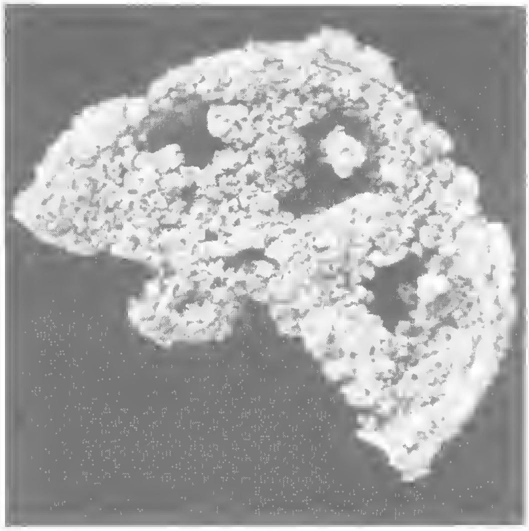


FIG. 26. *Chatsworthia spinosa* sp. nov., NMVP108990, paratype, internal surface, x6.

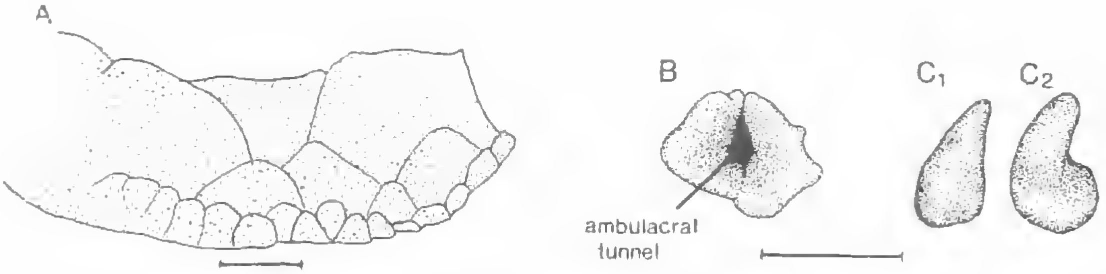


FIG. 27. *Chatsworthia spinosa* sp. nov., camera lucida drawings. A, QMF17948, peripheral rim plating in side view. B, QMF17946, view of one ambulacrum looking from the mouth cavity. C, reconstruction of one cover plate, based on NMVP108990 and QMF 17948. C1, external aspect. C2 internal aspect. Scale bars = 1 mm.

The phylogenetic placement of *Astrocystites* has been particularly difficult because there were no clear intermediate forms linking it to other echinoderm groups. It was therefore difficult to establish homologies. The discovery of a primitive form of edrioblastoid from the median Upper Cambrian of Australia bridges the gap between the mid Ordovician *Astrocystites* and certain edrioasteroids, making the phylogenetic placement of edrioblastoids much clearer.

PHYLOGENETIC POSITION OF EDRIOBLASTOIDS

Even prior to discovery of *Cambroblastus* the link between edrioblastoids and blastoids (Hudson, 1925,1927; Fay, 1967) seemed untenable. The lack of brachioles and a homologue of the hydrospire system and lancet plate clearly distinguished edrioblastoids. Furthermore, the ancestry of blastoids is now generally agreed to lie with coronates such as *Stephanocrinus* (Sprinkle, 1980b, Brett *et al.*, 1983, Smith, 1984, Donovan & Paul, 1985, Paul, 1988) which resemble edrioblastoids even less.

Two Cambrian groups seem worthy of consideration as possible ancestors to edrioblastoids, namely eocrinoids and edrioasteroids. Many eocrinoids possess a polyplated stalk like that of *Cambroblastus* that is differentiated from a bud- like theca. They also have the rudiments of an organised thecal plating with differentiated circlets of plates including basals, just as in *Cambroblastus*. The ambulacral arrangement is much different, however. Eocrinoids have short ambulacra restricted to the oral pole and these give rise to slender brachioles. Brachioles attach to the flooring plates and are believed to be homologous with the cover plate series seen in primitive echinoderms (Paul & Smith, 1984). The absence of any indication of brachioles in the Upper Cambrian edrioblastoid is strong evidence that edrioblastoids are not specialised offshoots from some eocrinoid lineage.

The derivation of edrioblastoids from edrioasteroids seems much more likely. The ambulacral structure in *Cambroblastus* is very like that in edrioasteroids, with large primary cover plates roofing a broad and deep food groove that covers much of the oral surface. The reduction of flooring plates to a single mouth angle plate, as occurs in *Astrocystites* has its precedents amongst edrioasteroids, since this is precisely what occurs in cyathocystids and probably also in rhenopyrgids. Furthermore, both of these edrioasteroid groups have elongate thecae, with the aboral surface developed into a stalk. In the

FIG. 28. *Chatsworthia spinosa* sp. nov. reconstruction; interambulacral plating stippled.

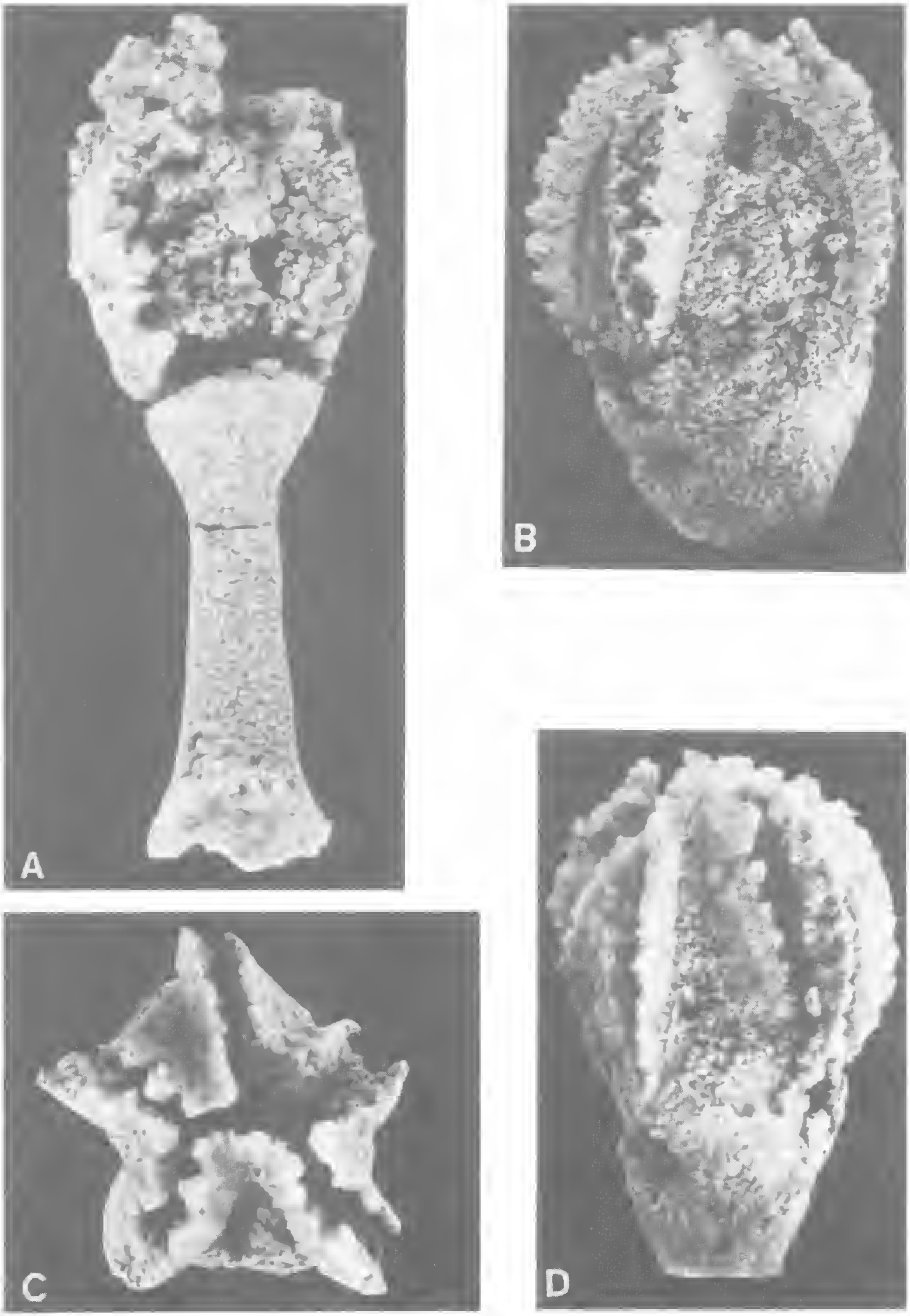
cyathocystids the stalk is a single (?fused) calcite plate in the form of a long cylindrical tube (Bockelie & Paul, 1983), while in rhenopyrgids the stalk is composed of imbricate plates. One of us has argued previously (Smith, 1986) that the stalk in rhenopyrgids is homologous with the aboral plated surface in stromatocystitids and that the circum-oral plates at the top of the stalk are homologous with the peripheral rim plates in other edrioasteroids. If this is correct then the plated holdfast in *Cambroblastus* would be homologous with the large central plates in *Stromatocystites* or *Totiglobus* and the plated holdfast of smaller platelets homologous with the peripheral rim of submarginal platelets. *Cambroblastus* has a rigid basal part to its theca and a more flexible upper part. The lower part consists of 3 circlets of tesselate plates and from its position, between the extremities of the ambulacra and the flexible subambital zone of platelets, would appear to be a direct homologue of the peripheral rim plates of other edrioasteroids. The upper semi-flexible part of the theca is composed of interambulacral and ambulacral areas similar in arrangement to those found in other edrioasteroids, especially in the biserial arrangement of flooring plates and the large simple cover plates. Over the oral area the 5 primary cover plates meet centrally, exactly as they do in cyathocystids and rhenopyrgids.

Since the plating in *Cambroblastus* can be directly homologized with that of edrioasteroids (Fig. 34), whereas eocrinoids differ in the fundamental structure of their ambulacra, we believe edrioblastoids are derived forms of edrioasteroids. Three principal groups of edrioasteroids stem from a *Stromatocystites*-type ancestor (Smith, 1986): 1, Isorophida, which are disc-shaped encrusters with an unplated aboral surface; 2, Edrioasterida, which are globose bottom dwellers that have retained biserial flooring plates and have lost the central plating of the aboral surface; and 3, Cyathocystida which are turret-shaped forms which have formed a peduncle from the aboral plated surface and have reduced ambulacral plating to 5 interradially positioned flooring plates that carry multiple cover plates. Both edrioasterids (*Walcottidiscus*) and isorophids (*Chatsworthia*) had become differentiated by the median Upper Cambrian, but the earliest cyathocystids are mid Ordovician in age. Edrioblastoids have expanded their aboral surface into a stalk and in later forms reduced their ambulacral flooring plates to 5 interradial elements (the deltoids of *Astrocystites*). They are therefore likely to represent a sister group to the Cyathocystida. *Cambroblastus* seems to be too specialised to represent a common ancestor to either cyathocystids or rhenopyrgids however, although the reduction of flooring plates to the 5 primary plates is a putative synapomorphy of *Astrocystites* plus cyathocystids plus rhenopyrgids. Until intermediates linking rhenopyrgids, cyathocystids and primitive edrioblastoids are found, relationships of these 3 groups will remain problematic.

TRANSITION TO *ASTROCYSTITES*

Although *Cambroblastus* closely resembles *Astrocystites* in general organisation (both have a polyplated stalk, a bud-shaped theca dominated by large ambulacral plates that extend below the ambitus and are roofed by primary cover plates) it retains a number of primitive characteristics. Several morphological changes must have taken place in the evolution of *Astrocystites* from *Cambroblastus*. Firstly the thecal plating became simpler with the reduction to 5 basals and 5 radials. It also became completely rigid, flexibility along the adradial margins of the ambulacra apparently being lost. Ambulacral plating was also simplified with the loss of all but the first (interradially positioned) ambulacral flooring plate. This flooring plate expanded into the deltoid plate and its distal tips grew over the adoral portion of the radial plates. The simplification of thecal plating through the loss of circlets and all but the first formed ambulacral flooring plate is most likely to have been achieved through heterochrony, with the appearance of juvenile features in adult forms being the product of neoteny or paedamorphosis. Elongation of the primary oral plates into deltoids and the multiplication of coverplates would have occurred at a later stage.

A second major difference between *Cambroblastus* and *Astrocystites* is in the system of intrathecal pores developed along the adradial margin of the ambulacral groove on deltoid plates. No such system of pores is preserved in *Cambroblastus*, which would therefore appear to be a specialization of derived edrioblastoids. However, preservation is such that we cannot entirely rule out the possibility that minute pores were originally present but have become obliterated with silicification. The function of the pores in edrioblastoids has never been properly assessed. They could be the equivalent


A
B
C
D

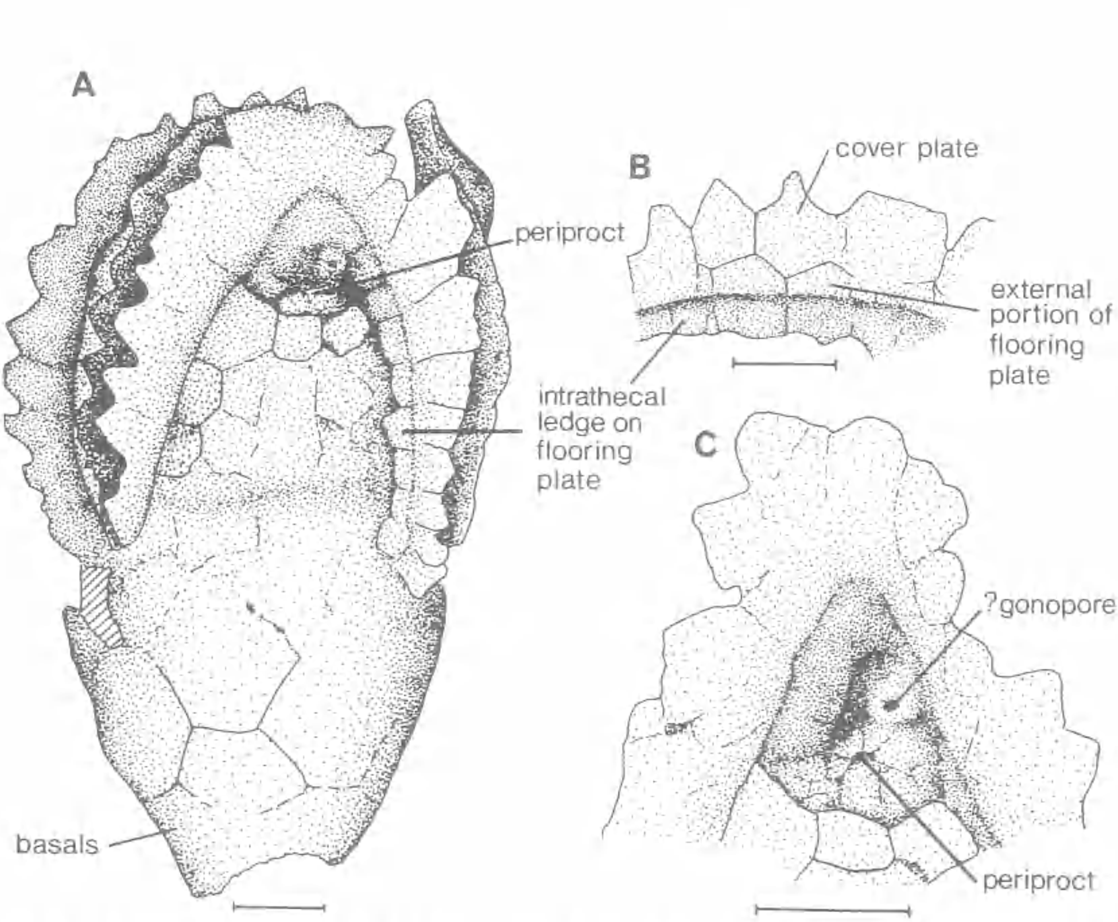


FIG. 30. *Cambroblastus enubilatus* sp. nov., QMF17872, holotype, camera lucida drawings. A, lateral view of posterior interray. B, lateral view of ambulacral plating in ambulacrum III. C, detail of periproctal region. Scale bars = 1 mm.

of the ampullar sutural pores in primitive edrioasteroids but these are absent from *Cambroblastus* as far as can be told and would have to represent an atavistic structure. Furthermore, they are not sutural pores, as in *Stromatocystites* or *Edrioaster*, but are a series of pores within a single ambulacral flooring plate. Whatever their function, they are probably unique to *Astrocystites*.

The only other significant difference is in the organization of stalk plating. Whereas there appears to be no clear lineation to stalk plating in *Cambroblastus* the stalk of *Astrocystites* is made up of 5 columns of plates (although only the proximal part of the stem is known). This again is a specialization of *Astrocystites*.

Cambroblastus gen. nov.

ETYMOLOGY

From Cambrian and the Greek *blastos*, a bud, in allusion to the shape of the theca.

TYPE SPECIES

Cambroblastus enubilatus sp. nov.

AGE AND DISTRIBUTION

Median Upper Cambrian (Franconian) of Queensland.

FIG. 29. *Cambroblastus enubilatus* sp. nov. from the Chatsworth Limestone, median Upper Cambrian of Chatsworth. A, QMF17873, paratype in side view, x8 (see also Fig. 32). B-D, QMF17872, holotype. B, lateral view of posterior interradius, x7.5 (see also Fig. 30). C, oral view, x7.5 (see also Fig. 31). D, lateral view of ambulacra III and IV, x7.5. Silica replacements whitened with ammonium chloride sublimate.

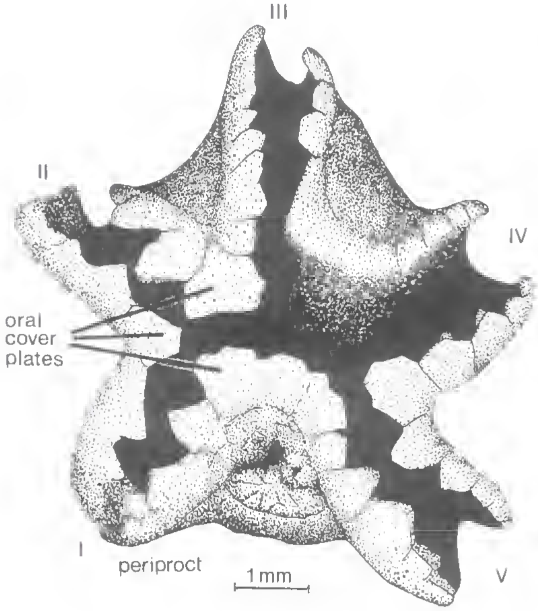


FIG. 31. *Cambroblastus enubilatus* sp. nov., QMF17872, holotype, camera lucida drawing of the oral region.

DIAGNOSIS

An edrioblastoid with an irregular polyplated stalk, 3 irregular cycles of thecal plating and ambulacra composed of biserially arranged flooring plates bearing simple cover plates. No intrathecal pores to the ambulacral grooves.

REMARKS

This genus is sister group to the Ordovician edrioblastoid *Astrocystites* on account of its very similar thecal shape and ambulacral organisation and its polyplated holdfast. It differs from that genus in having an additional circlet of thecal plates between the radials and basals, in having multiple biserial flooring plates to each ambulacrum rather than a single oral plate (deltoid), and no system of pores along the margins of the ambulacral grooves. Furthermore, the plating of the stalk is less well organised in *Cambroblastus*.

Cambroblastus enubilatus sp. nov.
(Figs 29-33)

ETYMOLOGY

Latin *enubilatus*, freed from clouds, an allusion to its importance in revealing the origins of edrioblastoids.

TYPES

Holotype QMF17872, paratype QMF17873; no other specimens are known.

AGE AND OCCURRENCE

Both specimens come from locality K204 of Shergold (1982), from a grey, 4 m thick unit of the Chatsworth Limestone, 3.5 km south of Chatsworth homestead, 60 km southeast of Duchess, western Queensland. *Peichiashania secunda-Prochuangia glabella* Assemblage Zone, median Upper Cambrian (Franconian).

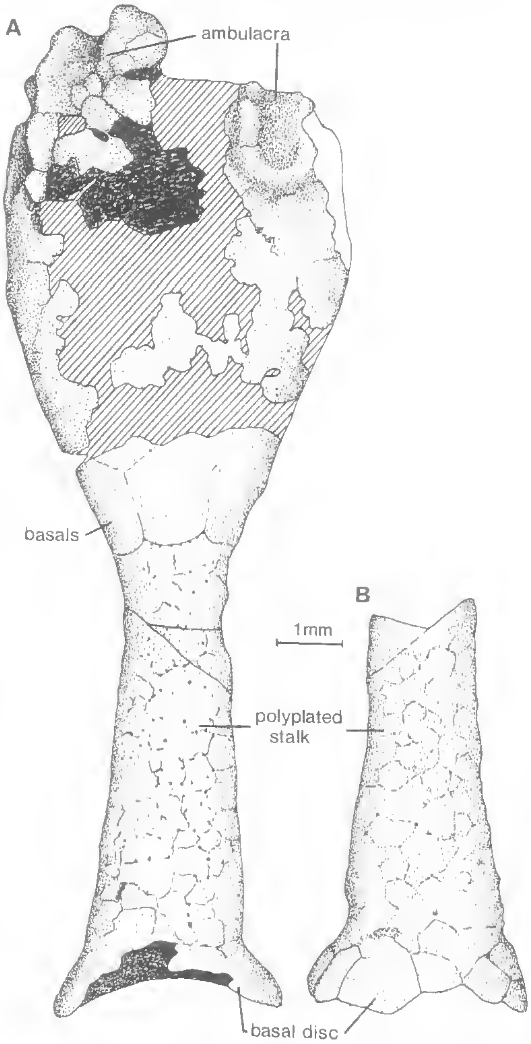


FIG. 32. *Cambroblastus enubilatus* sp. nov., QMF17873, paratype, camera lucida drawings. A, lateral view of complete specimen. Hatched lines = missing; black = plate surface badly etched. B, obverse of stalk.

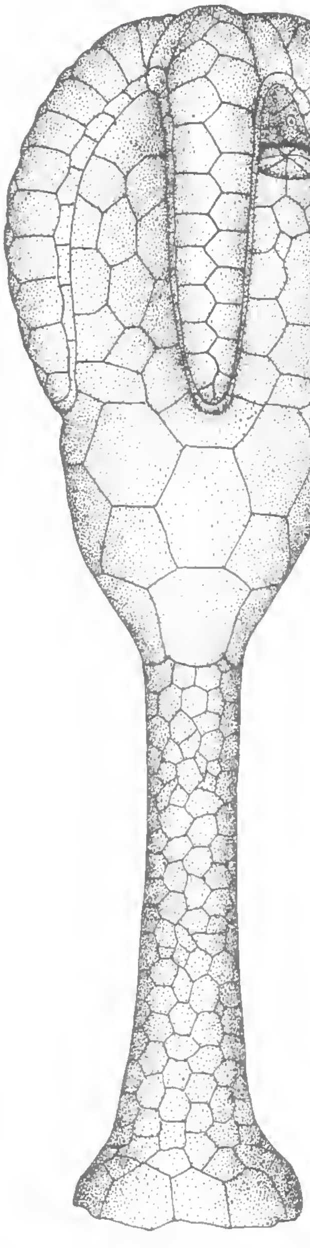


FIG. 33. *Cambroblastus enubilatus* sp. nov. reconstruction.

DIAGNOSIS

As for genus.

DESCRIPTION

The theca is 10-11 mm long and 6-7 mm in maximum diameter with the widest part being slightly above mid-height. The stem is 5.5 mm long and 1.5-2 mm wide, with a flared base (Fig. 29A). The theca tapers gradually to the stalk and has a rounded apex. In oral view the theca is rounded pentagonal in outline, with the angles formed by the prominent ambulacra (Fig. 29C). Interradial zones are concave. The mouth lies at the apex of the theca and the periproct close to the apex in the posterior interambulacrum (Fig. 30A). There are 5 large and prominent ambulacra stet that meet in a 2:1:2 pattern at the apex (Figs 29C, 31). Ambulacra are c. 2 mm wide at the apex and taper slightly to a broad rounded point situated a little below the ambitus. The ambulacral groove is completely roofed over by a series of simple cover plates. There are 9 or 10 cover plates in each column. These are largest at the apex and become progressively smaller distally (Fig. 30A,B). Cover plates are tall and form a spacious vaulted canopy to the ambulacral groove. The cover plates fit together tightly with no sutural gaps. They interlock along a zig-zag perradial suture. Individual plates are pentagonal in outline and have a single moderately well-developed sagittal strut on their inner face. The suture between cover plates and flooring plates is nowhere clearly seen. In ambulacrum II the cover plates appear to alternate with the flooring plates (Fig. 30B). Elswhere they may sit more directly above the flooring plates, although plate boundaries are nowhere clear. No secondary cover plates are present. Over the oral area there are 5 large cover plates that meet centrally, one from each interradius (Fig. 31). The posterior interradius may, however, have 2 such plates, to judge from the plate outline. These are the oral plates and the smaller adjacent cover plates may attach directly to them.

The floor to the ambulacral groove is U-shaped and smooth, with slight undulations marking the plate boundaries. Flooring plates are biserial and in places the sutures have been preferentially etched. However, no sutural pores are consistently developed and in less corroded ambulacra no pores whatsoever can be seen. We therefore believe that pores were either not present in the ambulacral groove or small and obliterated by silicification. Flooring plates are exposed along the adradial margin on the outer side of the ambulacra (Fig. 30B). Beneath the exposed portion of the flooring plates a distinct concave facet runs the length of the ambulacrum (Fig. 30A). This is the intrathecal section of the flooring plates and is an imbrication flange on which the interambulacral plates rest. In the posterior interambulacrum of the holotype, interambulacral

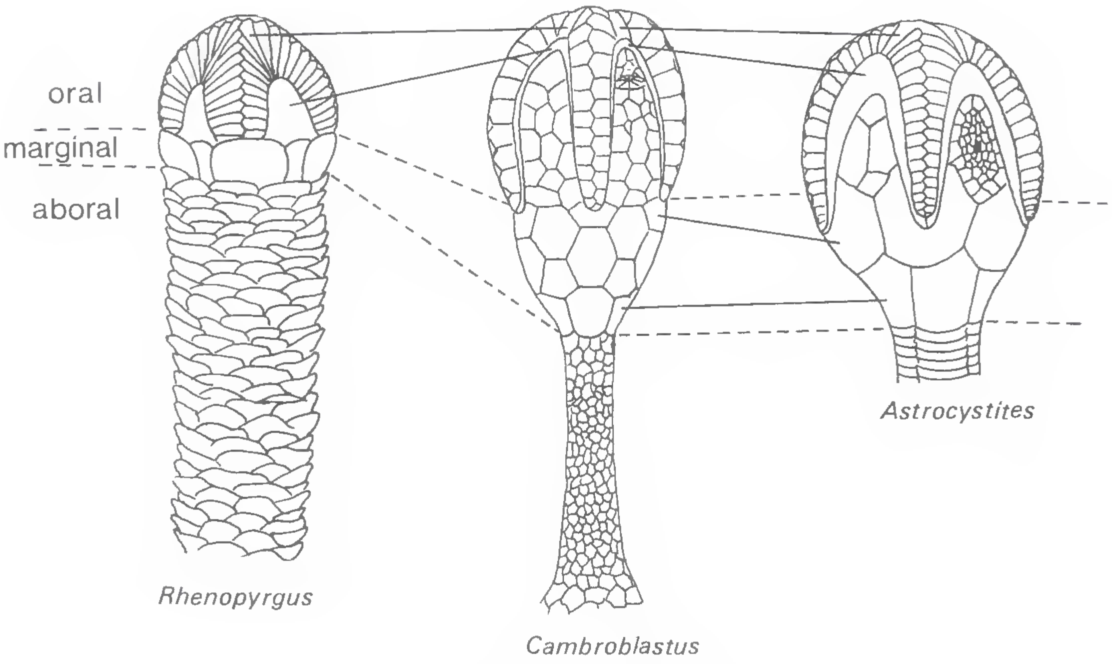


FIG. 34. Diagram indicating the homologous regions of plating in rhenopyrgids (*Rhenopyrgus*), *Cambroblastus*, and the Ordovician edrioblastoid *Astrocystites*.

plates are preserved in position against ambulacrum I, covering the facet, but have slid off the flooring plates of ambulacrum V on the other side to reveal the concave facet (Figs 29B, 30A). This suggests that the ambulacral/interambulacral boundary was imbricate not rigid and that the ambulacral flooring plates had some limited degree of flexibility. The sutures between flooring plates are well seen in the intrathecal section.

Interambulacral plating, best seen in the posterior interambulacrum (Fig. 29B, 30A), consists of a pavement of small polygonal plates with slightly swollen centres. These are 3-5 abreast, reducing to a single plate adapically. There may be a single elongate plate in the centre of the posterior interambulacrum. The interambulacral plates tend to hold together even though they are displaced from the adradial suture, suggesting that they were firmly bound together.

The periproct opens close to the oral area in the posterior interambulacrum (Fig. 30A,C). It faces towards the apex and is set back on a ledge. It is composed of a low cone of wedge-shaped plates, relatively few in number. Above the periproct and close to ambulacrum V is a small conical structure with a central depression (Fig. 30C) interpreted as the gonopore. No trace of the hydropore is seen, probably because of the coarse preservation.

The lower part of the theca is cup-like and appears to have been rigid. Plate boundaries are obscured except in the posterior part of the theca (Figs 29B, 30A). Here traces of 3 circlets of plates are visible. In the paratype there are 3 plates forming the base of the cup on one side (Figs 29A, 32) and, by inference, there must therefore be a basal circlet of 5 plates, which we homologise with the basals of *Astrocystites*. Above this, in the holotype are large hexagonal plates. Because only traces of sutures can be distinguished we are not certain of a regular pentameral pattern to this plating but there are 2 further circlets of polygonal plates above the basals. Some of these appear to be slightly concave and all are covered in a fine retiform ornament. At the base of the ambulacra an indistinctly defined plate may be the homologue to the radials in *Astrocystites*.

The stalk (Fig. 29A) is cylindrical, narrowest immediately beneath the theca, and expanding slightly towards the base. The surface appears

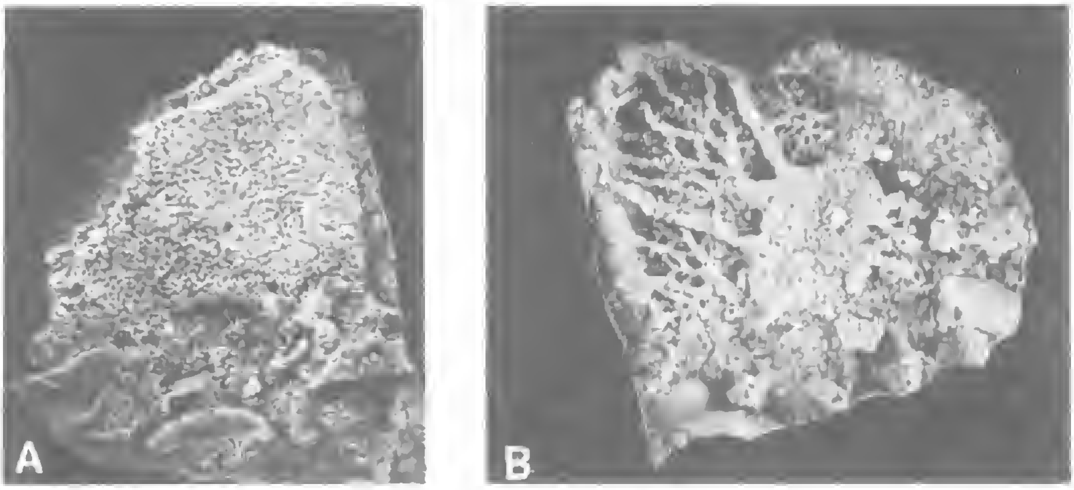


FIG. 35. Incertae sedis echinoderm fragment, QMF 17859, early Middle Cambrian from QP243 near Cornford Bore, x4. A, external surface. B, internal surface. Latex casts whitened with ammonium chloride sublimate.

different in texture to the theca, being much more granular and with many small pits. As a number of these pits appear to be linearly arranged we interpret them as traces of plate boundaries and the stalk to be composed of a relatively large number of small granular platelets. Towards the base these platelets become better defined and are polygonal in outline. At the base the stalk flares outwards into a cup-shaped holdfast of large polygonal plates (Fig. 32). The stalk is broken at the bottom and the full extent and shape of this holdfast remains unknown.

REMARKS

A comparison of this species to the only other known edrioblastoid, *Astrocystites*, has been

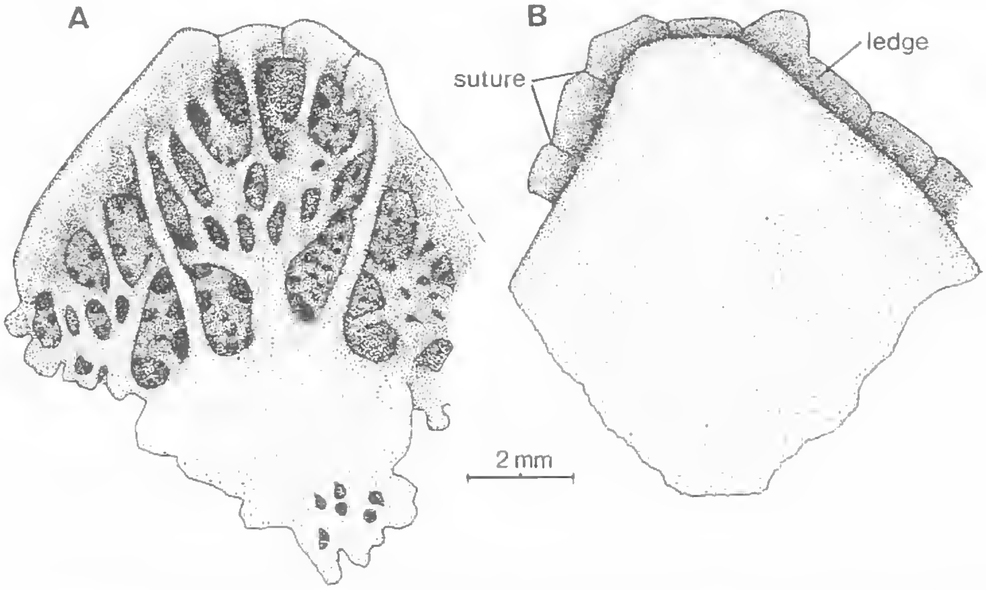


FIG. 36. Incertae sedis echinoderm fragment, QMF 17859, camera lucida drawings of internal (A) and external (B) surfaces.

given above and its phylogenetic position has also been dealt with fully. *Cambroblastus* was an erect, medium-level, suspension feeder using its ambulacra to capture suspended food particles. The stalk, which is relatively well-developed for Cambrian echinoderms, would have elevated the food capturing surfaces well above the substratum. *Cambroblastus* must have been attached to a substratum by its basal disc but, because only part of this is known, we are not sure as to how fixation was achieved. However, the shape of the basal disc is reminiscent of basal attachment discs of *Echinosphaerites* for attachment to hard substrata, and is unlikely to have been a rootlet structure for attachment within unconsolidated sediment. The apparently tesselate nature of the stalk platelets suggests that the stalk was relatively stiff and inflexible, unlike the imbricate stalk of rhenopyrgid edrioasteroids. Furthermore the stalk is relatively robust and has held together well, not having collapsed during fossilization. Both observations indicate that the stalk of *Cambroblastus* was more or less rigid and not extensible.

The broad imbricate facet between the flooring plates and the interambulacral plates implies that this boundary was flexible and that a large degree of movement was permitted between the two plate systems. Interambulacral areas are often separated from the adradial suture and are also variable in width (Fig. 29B,C,D). Furthermore, there is a distinct change between the lower cup- like portion of the theca, where plates are rigidly sutured, and the rather irregularly concave surfaces of the interambulacra between the arms. The flexibility between ambulacral flooring plates and interambulacral regions suggests to us that the ambulacra retained a certain amount of movement and that the food groove could be widened or closed by lowering or raising the flooring plates.

The absence of pores in the floor of the food groove requires that the water vascular system. presumably lying in the floor of the groove, lacked internal ampullae.

Incertae sedis
(Figs 35, 36)

MATERIAL
A single specimen, part and counterpart preserved as a mould in silica. QMF 17859a/b.

AGE AND OCCURRENCE
From chert beds of the Yelvertoft Member, Beetle Creek Formation, early Middle Cambrian, exposed on the northern flank of a low rise some 500 m south of the bore at Yaringa Creek, 50 km west-southwest of Mount Isa, western Queensland (GR 980965).

DESCRIPTION
The specimen is 10 mm x 12 mm, although the posterior(?) edge is fractured and missing. It has a narrow anterior border and 2 long straight sides that diverge at c. 80°. The external surface (Figs 35A, 36B) shows a flat, unornamented platform surrounded by a 1 mm wide ledge. This ledge is concave, dipping steeply from the platform before levelling out. It is crossed by vertical sutures approximately 0.8-1.0 mm apart. There is a central plate on the anterior border and adjacent plates occupy each of the angles. No sutures are seen on the platform.

The interior of the specimen shows a steeply dipping marginal rim surrounding a crescentic region of labyrinthine struts (Figs 35B, 36A). There is a central platform towards the posterior of the specimen. The rim is crossed by vertical sutures, at least anteriorly. Struts from the labyrinthine region run to the centre of each marginal plate. The anterior struts are rather short and dip into the labyrinthine region but there are 2 long struts that run from the side walls right to the posterior platform without branching. The floor of the labyrinthine region is pitted and the specimen must have been exceedingly thin at these points. The posterior platform is flat and smooth. Towards the posterior there are 6 small (0.2 mm diameter) pores. It is not known whether these perforate the plate as the corresponding region is not seen in the counterpart. No sutures are seen in either the labyrinthine region or the posterior platform.

REMARKS
This fragment is an enigma. We feel confident that it is echinoderm, even though calcite plating is not preserved. This is because of the presence of plate boundaries along the peripheral ledge. The absence of sutures in the main body of the plate suggests to us that the fragment is a composite element, constructed of several plates fused together. The peripheral flange and shape of this element are reminiscent of large interradial first ambulacral plates; the flange being an adradial ledge either formed of fused ambulacral flooring plates or directly flooring the am-

bulacra. Large deltoid plates, situated interradially and bearing ambulacral structures, are known in edrioasteroids, blastoids, parablastoids and edrioblastoids. The interradial plates in edrioasteroids form the oral frame and are suspected of being formed from fused ambulacral flooring plates (Bell, 1976, Smith, 1986). However, they are much smaller and none is known to have such a distinctive labyrinthine interior. In edrioblastoids the interradial deltoids are also supposedly composed of fused ambulacral flooring plates (Mintz, 1970, Bell, 1980) and here the plate is large with an adradial ledge. However, such deltoid plates are known only in the Middle Ordovician *Astrocystites* and were apparently absent in the Late Cambrian *Cambroblastus*. The deltoids in blastoids carry part of the hydrospire system and are not closely comparable. The deltoid in parablastoids is a large plate perforated by a system of canals termed cataspires (Sprinkle, 1973, Paul & Cope, 1982). It does not underlie the ambulacra but abuts the flooring plate system and no species is known to have a labyrinthine internal plate ornamentation. Because it may represent an interradial plate of fused ambulacra we suspect it might be some form of edrioasteroid derivative, but it represents a major departure in form from any reported echinoderm group.

The crescentic zone of labyrinthine struts creates an extremely thin-walled surface and we believe that this may be an adaptation for gaseous exchange. The struts provide strengthening support to the theca, bracing the ambulacral zones, while the pits are sites of gaseous exchange. Extreme thinning of calcitic plates associated with gaseous exchange is a common feature in many echinoderm groups. Amongst cystoids, for example, thin-walled regions of the plate are found in paracrinoids (deep pits), diploporites (the exterior of haplopores is a thin membrane of calcite) and dichoporites (where tube-like passageways from the interior run immediately beneath the surface of the plate). The arrangement of pits and struts in such an irregular manner rules out the presence of any sophisticated circulatory system as in most cystoids. Gaseous exchange must have taken place through simple diffusion across the thin plate

'Subclass SOMASTEROIDEA'

Family ARCHEGONASTERIDAE Spencer, 1951

Archegonaster Jaekel, 1923

TYPE SPECIES

Archegonaster pentagonus Spencer, 1951

Archegonaster pentagonus Spencer, 1951
(Figs 37-51)

Archegonaster pentagonus Spencer, 1951, p. 101, figs 9, 10, 12-15, 34, 37-40, 54, 55.

Archegonaster pentagonus Spencer; Spencer & Wright, 1966, p. U41, fig. 39C.

Archegonaster pentagonus Spencer; Smith, 1988b, p. 89, pl. 7.1, fig. 4, pl.7.2, fig. 6.

MATERIAL

The Narodni Museum, Prague houses 65 specimens, including the types.

AGE AND OCCURRENCE

All material comes from the Llanvirn Sarka Formation of the Osek district, Prague, Czechoslovakia.

DESCRIPTION

Archegonaster is a pentastellate echinoderm with a stout marginal frame of ossicles and narrow projecting arms (Fig. 37). There is no separation between disc and arms, the two merging imperceptibly into one another. Its size is difficult to estimate since so many specimens are incomplete or distorted. The most complete specimen (Fig. 37) has a radial length of 35 mm and an interradial/radial diameter of 60 mm, but the tips of its arms are missing. Specimens cover a large size range, from about 15 mm radial length (Fig. 49B) to around 50 mm. The body is flattened.

Ambulacra. These are composed of biserially arranged ambulacral ossicles (=flooring plates) arranged alternately and forming an open U-shaped channel (Figs 38-40). In oral view they appear as T-shaped ossicles, measuring about 3 mm perradially and with a 2 mm transverse bar in larger specimens (Figs 40A, 41B-E). The perradial suture is virtually straight and successive ambulacral plates overlap one another, the distal part of one plate passing beneath the proximal part of the next distal plate. About one third of the plate imbricates beneath the adjacent ambulacral plate. The perradial face, forming the ambulacral groove, is relatively smooth and slightly depressed centrally. The distal portion of the plate is more tapered and composed of denser stereom: this is the portion that passes underneath the next distal plate. There is a well marked rim to the top of the ambulacral groove. This runs from the proximal end of the plate to the transverse bar, where it ends abruptly at a notch (Fig. 40A). Presumably, this is the notch for the lateral branch of the radial water vessel leading to a tube foot. In larger specimens the floor to this notch has a small pit. When ambulacral plates are in life position (Figs 38E, 41B-E) the distal wall of the notch for the radial water vessel is formed by the proximal edge of the succeeding ambulacral plate. The transverse bar is tall and narrow, with steeply sloping sides. The ridge to the ambulacral groove continues along the top of this bar. At its abradial end the transverse bar is tripartite, with a large flattish central face that slopes outwards (the articulation face for the adambulacral ossicle) and two narrow rims marking the edges of proximal and distal podial basins (Figs 39G, 40C). The articulation face expands aborally and in some may be slightly convex, though it is usually flat. The flanges on either side are steeply dipping and flare out towards their base. The flange on the distal face is considerably better developed than that on the proximal face, which hardly flares out at all (Fig. 40A). Thus only the proximal part of each podial basin is floored and the narrow rims presumably mark the site of tube-foot attachment.

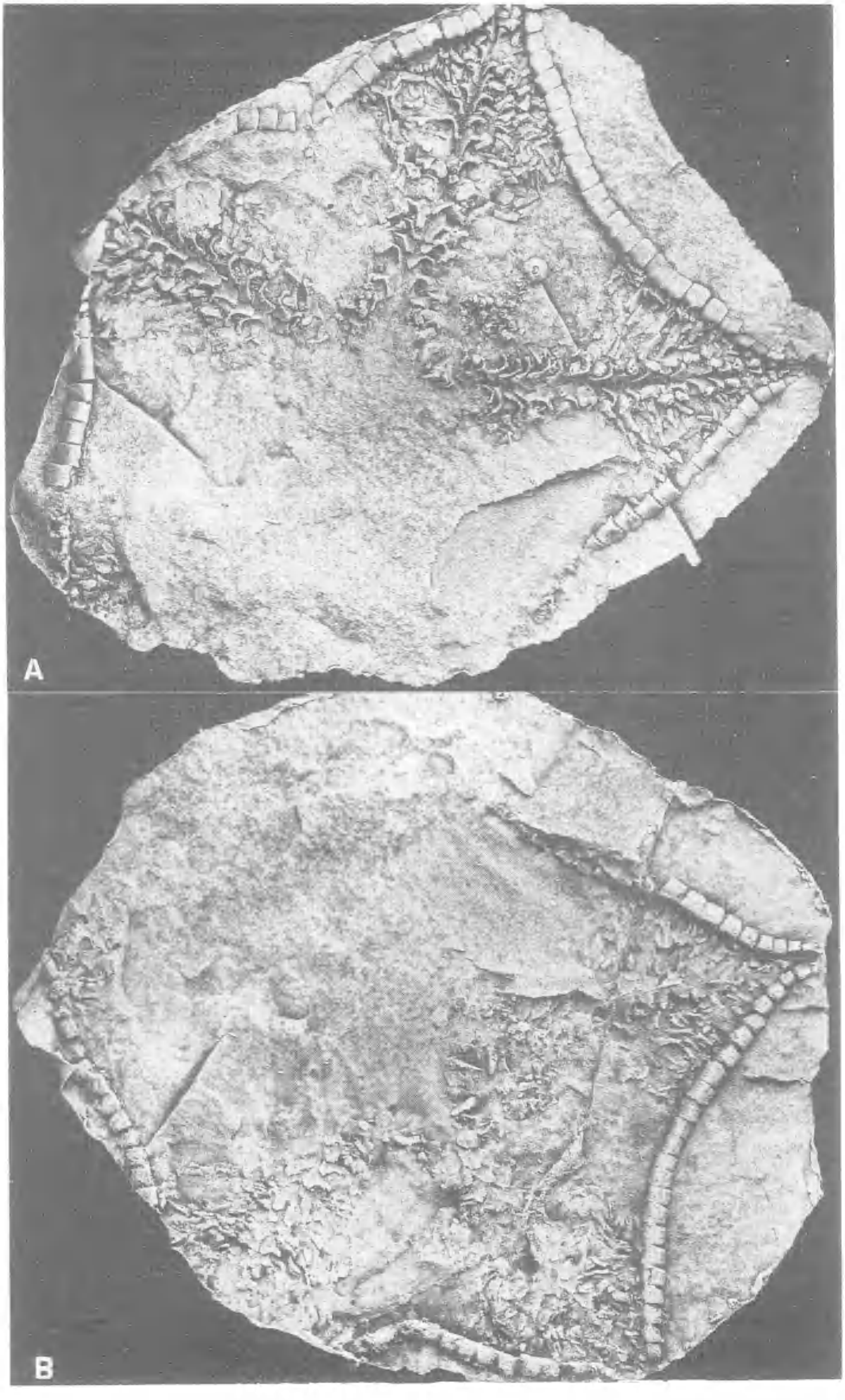
In aboral aspect the ambulacral plates are also T-shaped, with the transverse bar generally appearing much more clearly tripartite at its tip (Figs 40B, 41A). The perradial zone is rather flat and smooth, there being no evidence for dorsal inter-ambulacral muscle attachment sites. The proximal end of each ossicle is more pointed than the distal end and is marked off from the rest of the plate by a small rim. This rim becomes progressively more pronounced in plates towards the mouth and marks the limit of plate imbrication. The imbrication surface is inclined away from the perradius. The outer part of the plate also slopes downwards away from the perradius. The three regions at the tip of the transverse bar correspond to the central articulation face for the lateral arm plate and the two lateral flanges flooring the podial basins. As seen orally, the distal flange is much better developed than the proximal flange. The two flanges form a rim to the transverse bar.

The way in which opposite plates articulate perradially is not clear. There is no evidence for one series having over ridden the other or for overlapping of alternate plates. The perradial edge of ambulacral plates is thin and no tongue and groove structure could be identified. As the perradial line is virtually straight the ambulacral plates may simply have abutted along a narrow face.

In juvenile specimens, or towards the arm tips, the ambulacral plates become less strongly imbricate and more squarish in outline with a less pronounced transverse bar (Figs 40D,49 C).

Adambulacrals. Ossicles that articulate onto the ambulacral (flooring) plates are called adambulacrals in asteroids and lateral arm plates in ophiuroids. As both structures are homologous we choose to refer to such plates as adambulacrals. In *Archegonaster* the adambulacrals have a complex form, best understood by examining the camera lucida drawings that show the plate in different orientations (Fig. 42). The ossicle is L-shaped in side view and more irregular in adradial (i.e. the face that articulates with the ambulacral plate) and abradial (i.e. distal to the articulation facet) aspects. The ossicle has a laterally flattened shaft, articulating onto the ambulacral plate at its base, a swollen head and a laterally flattened abradial projection which articulates with the first virgal distally (the virgal projection). Short (1 mm) spines attach to the head (Fig. 41A). The proximal face of the shaft has a median ridge running up the length of the shaft (Fig. 42A). There is a clearly defined pit on the adradial side of this ridge towards the head of the shaft. This is presumably a muscle pit. The abradial edge of the shaft may have a small projection or flange beneath the main abradial projection, but only in larger ossicles close to the mouth. It is laterally flattened but never achieves the size of the virgal projection. The virgal projection is square-ended and compressed in the proximal/distal plane. It has a smoothly rounded distal face but is flatter or slightly concave on its proximal face and bears shallow grooves. The upper edge of the virgal projection is a well-defined rim in larger ossicles and this is separated from the median ridge of the shaft by a clear notch. The distal face has a prominent flattish platform forming the head. The upper (adoral) face of this platform carries 6 or 7 spines. The spines are largest on the proximal end and decrease in size significantly towards the distal end (i.e. towards the virgal projection). In oral view the spines sit in slight

FIG. 37. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia. A,B, NM EH30. A, oral. B, aboral. Latex casts whitened with ammonium chloride sublimate, x2.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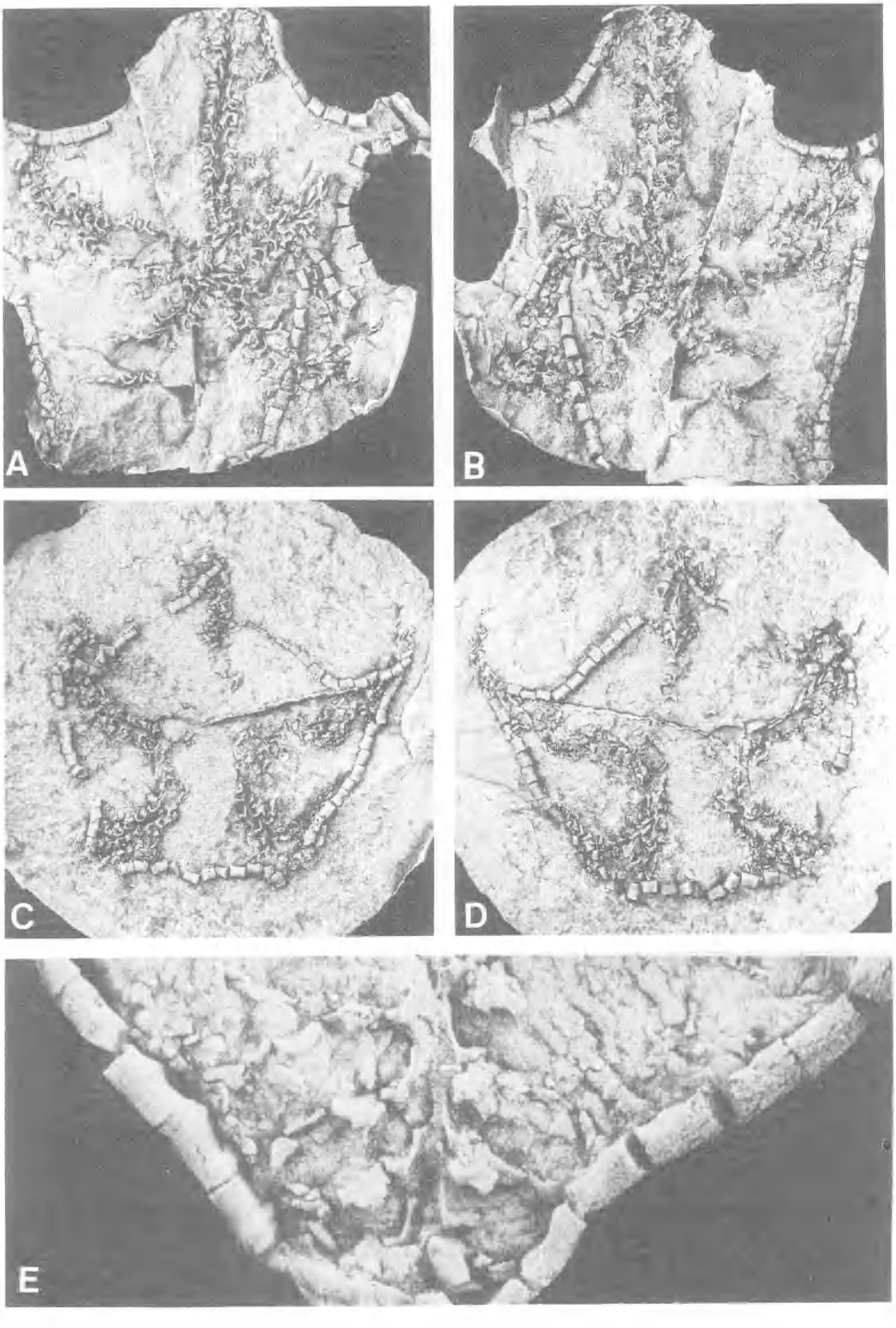
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depressions, the largest being proximal at the heel of the L-shaped plate.

Towards the mouth, the adambulacral ossicles become more slender and elongate along both the shaft and the virgal projection, while towards the arm tips the adambulacrals are much more block-like, with hardly any shaft or virgal projection. In the outer part of the ambulacra these adambulacrals attach directly to the marginal ossicles.

Interradial plating. The interradial zone, lying between the adambulacrals of the ambulacra and the marginal ring, is a complex, plated surface and commonly disrupted by post-mortem decay. Towards the tips of the ambulacra interradial plating is absent and the adambulacrals attach directly to the marginal ossicles (Figs 43C, 49C). At the interradius plating is also absent, leaving wedge-shaped uncalcified zones (Figs 37, 38A-D,43A,B). In between these two regions the adambulacrals are connected to the marginal ossicles via one or more slender rod-shaped plates termed virgals (Fig. 43). The number of virgals in a row increases towards the centre as the interradial space becomes broader. The first virgal attaches to the abradial projection on the lateral arm plate (Figs 43C, 45, 46) and is vertically orientated with slightly expanded ends. The distal face is smoothly rounded, with a central ridge that is continuous with a corresponding ridge on the lateral arm plate. The proximal face is flat or slightly concave and has spoon-shaped depressions at each end, possibly the site of muscle attachment (Fig. 44). The ends of the plate are flat suture faces. Up to 5 other virgals are present in the row (Fig. 46). These are generally similar in shape but some may fork abradially and the lower edge is often stepped (Fig. 44B). Those plates that fork show a double suture at one end and the ridge on the distal face also branches. Some plates have their plane of flattening rotated between adradial and abradial ends.

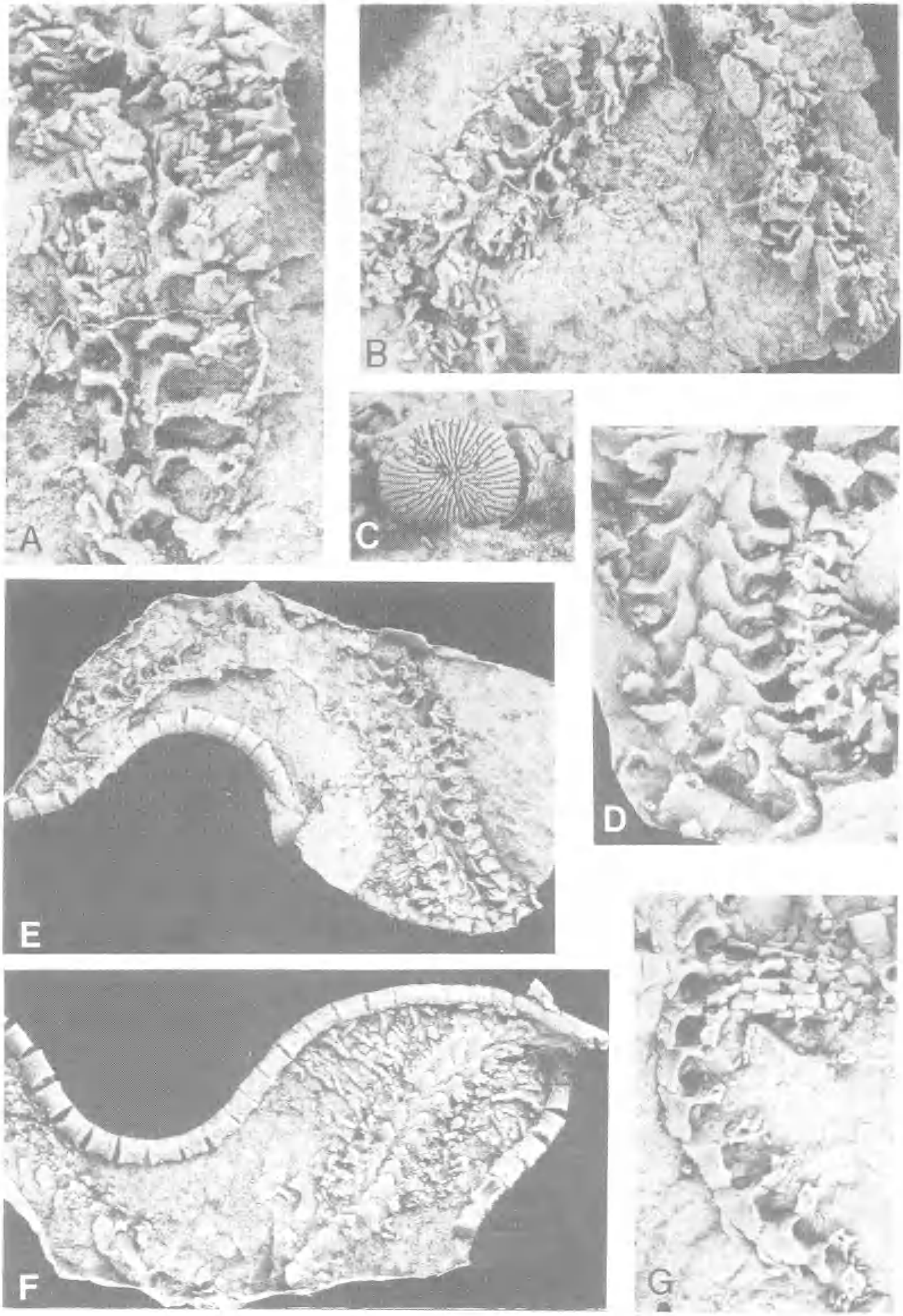
The rows of vertically elongate virgals are separated by rows of intervirgal plates (Figs 38E, 39F, 41C,D, 43C, 45, 46). These are more irregular in shape, some cross-shaped with four sutural faces. Where virgals are well preserved there is always an aboral set of plates that attach to the inner edge of the virgal row (Fig. 45). The first of these also attaches to the abradial edge of the lateral arm plate (Figs 41C, 45A). In the best preserved specimens (Fig. 39E,F) these plates form an almost complete covering to the interradial regions. There is a suggestion that the virgals form vertical ribs with the intervirgals lying flatter in the spaces in between. However, it is possible that the intervirgals are only connected to one side of the virgals and do not link adjacent virgal rows.

Mouth frame plates. The 3 most adoral ambulacral plates in each column are modified in *Archegonaster* into a jaw. Although a few specimens show large gaps down the perradial line of ambulacra (buccal slits of Spencer, 1951), this we interpret as post-mortem artefact. In well-preserved individuals only the first 2 ambulacral plates are completely separated from one another at the perradius (Figs 37, 38A). The first ambulacral plate lies interradially and is elongate radially (Fig. 47D). It is always paired with the corresponding plate from the adjacent ambulacrum and is the most highly modified of the ambulacral plates. The second plate is stouter, more cylindrical and is set obliquely to both the first and the third and subsequent ambulacral plates. The third ambulacral plate is only slightly modified from the remaining ambulacral plates in that it has a stout proximal end. Opposing third ambulacrals meet along the perradius in life.

The first ambulacrals, or mouth angle plates, are flattish plates that abut interradially along their aboral edge (Fig. 47A). The aboral face is crossed by 2 grooves. The more proximal groove is clearly marked and Vs towards the interradius. This, by comparison with the jaws of Recent ophiuroids, is the site of the circum-oral nerve ring. There is a strong projection immediately distal to the nerve ring groove and a shallower groove distal to this projection, which marks the site of the circum-oesophageal water vessel ring. The distal portion of the aboral face is a ledge and the groove for the water vascular ring runs obliquely away from the interradius along the edge of this.

In lateral view the interradial face (Fig. $47A_2$) has a broad, relatively flat platform distally and a zone of pits and transverse bars proximally. This pitted zone is presumably the site of insertion of muscle or ligament that binds the pairs of

FIG. 38. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia. A,B, NM 41/83, x2. A, oral. B, aboral. C,D, NM 42/83, x2. C, oral. D, aboral. E, NM L10446, one ambulacrum showing ambulacrals, adambulacrals, virgals, intervirgals and marginals, x7. Latex casts whitened with ammonium chloride sublimate.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plates together interradially. The platform is smooth and is an abutment surface. The proximal bar is smooth, uniformly convex and set oblique to the aboral face. The perradial face in lateral

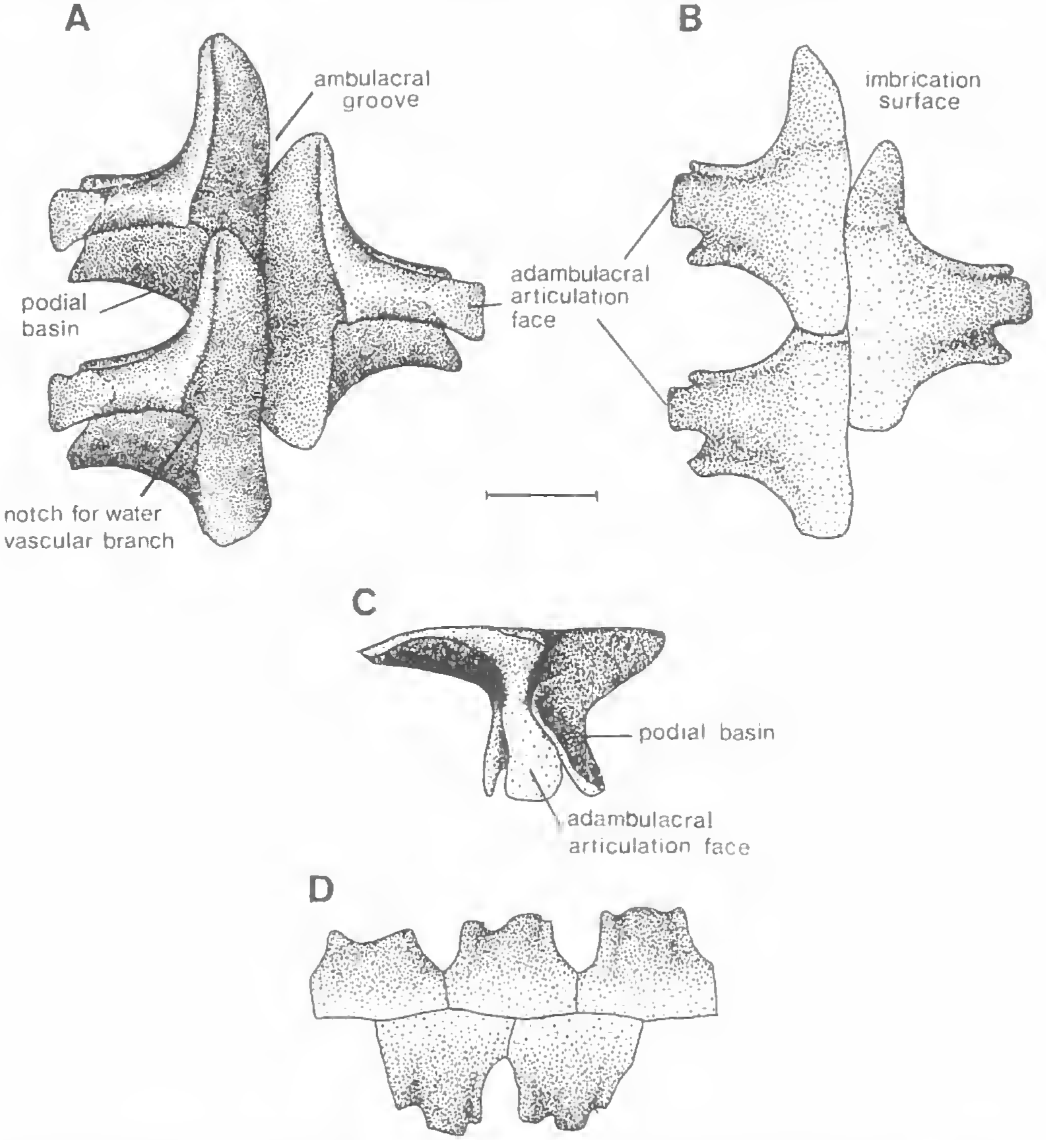
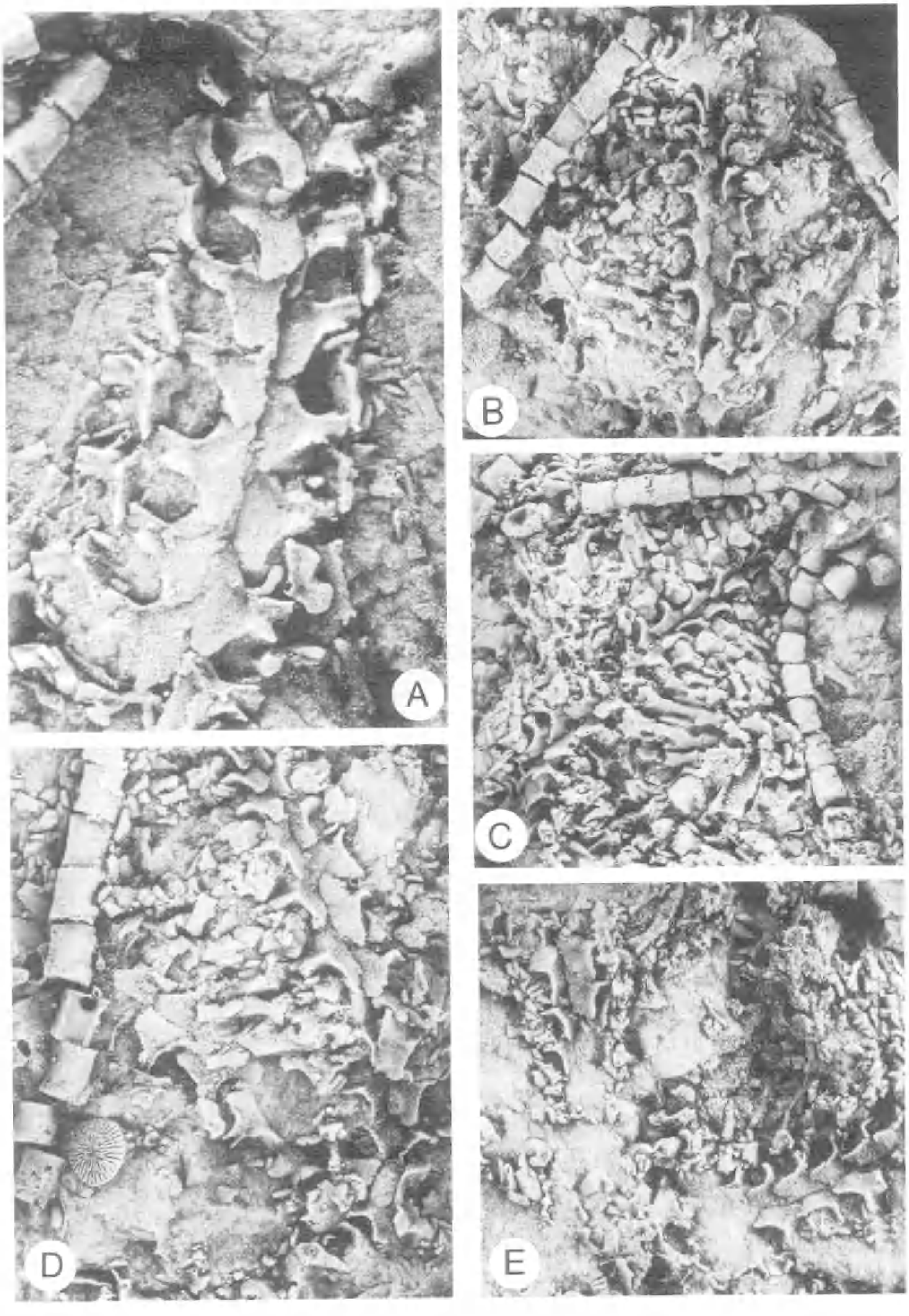


FIG. 40. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia. Camera lucida drawings of ambulacral plates. A, oral face of three plates, arm tip towards bottom (slightly restored from NM L10149). B, aboral face of 3 plates, arm tip towards bottom (slightly restored from NM L10438). C, abradial face of one plate arm tip towards right (from NM L10464). D, aboral face of 5 plates towards the arm tip, arm tip towards the left (based on NM L35050). Scale bar = 1 mm.

FIG. 39. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia. A-C, NM L10434. A, detail of ambulacral and adambulacral plates in oral view, x3.5. B, general view, x2. C, madreporite plate, x5. D, NM L10435, ambulacra with adambulacrals, x4. E,F, NM L10143, x2. E, oral. F, aboral (note interradial plating). G, NM L25454, lateral view of ambulacrals, aboral surface uppermost, with adambulacra and interradial plating, x3. Latex casts whitened with ammonium chloride sublimate.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view (Fig. 47A$_1$) has part of a podial basin distally and a thickened semi-cylindrical bar proximally. This proximal bar is smooth and uniformly convex. No spines were seen attaching to this proximal edge, but the plate could only be studied where the proximal plates had been disrupted and presumably mouth spines may easily have been dislodged or lost.

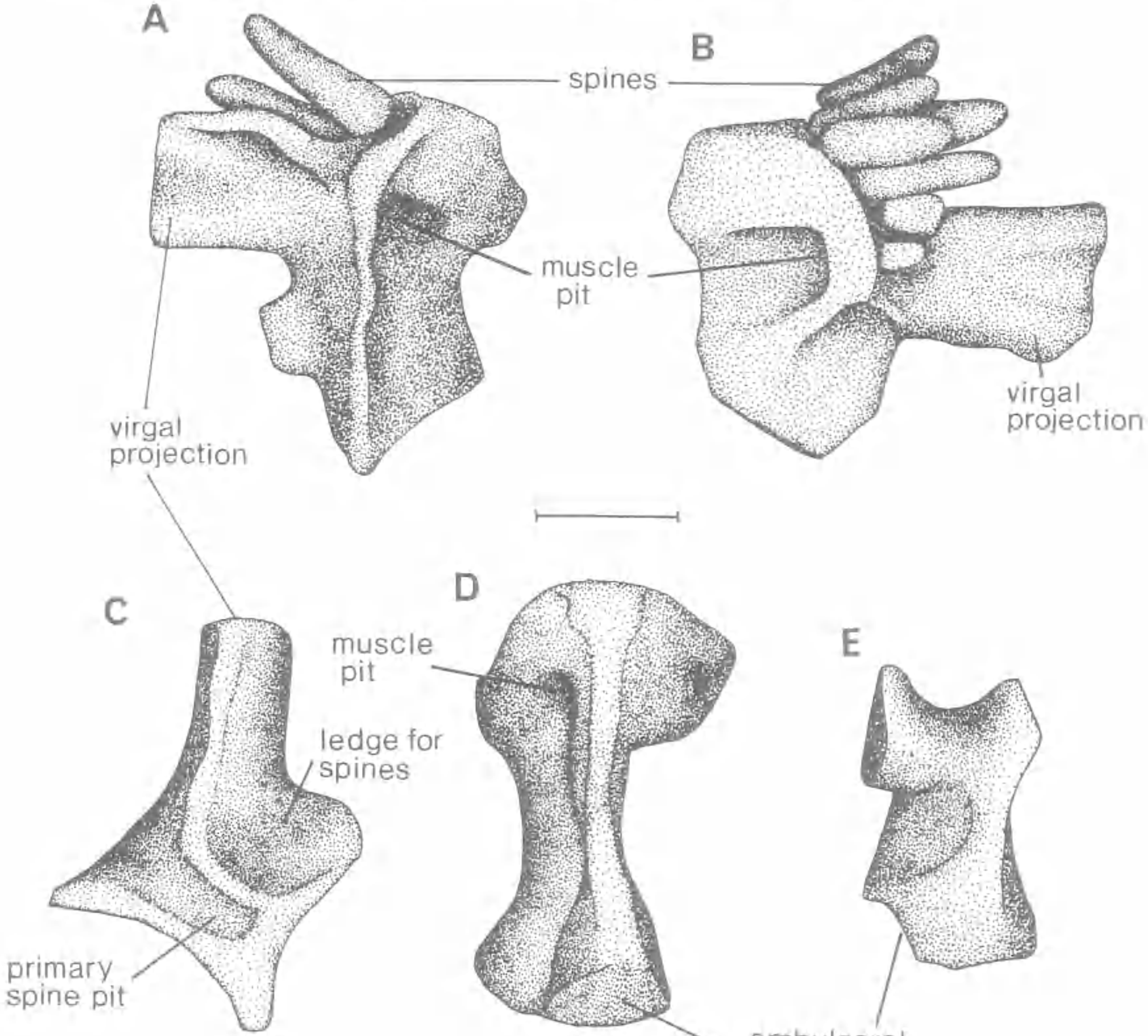


FIG. 42. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia, camera lucida drawings of adambulacra. A, lateral view of proximal face (NM L10438). B, lateral view of distal face (NM L10434). C, outer (oral) face (NM L10435). D, adradial face (NM L10435). E, inner (aboral) face (NM L10150). Scale bar = 1 mm and all to same scale.

FIG. 41. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia. A, NM L10438, aboral view of an ambulacrum with second ambulacral at the top. Note the adambulacrals seen in lateral view, x6. B, D, E, NM L10537. B, oral face of one arm, x3. D, same enlarged to show virgals and intervirgals, x5. E, adoral portions of two ambulacra in oral view, x3. C, NM 43/83, interradial plating in one arm, x3. Latex casts whitened with ammonium chloride sublimate.

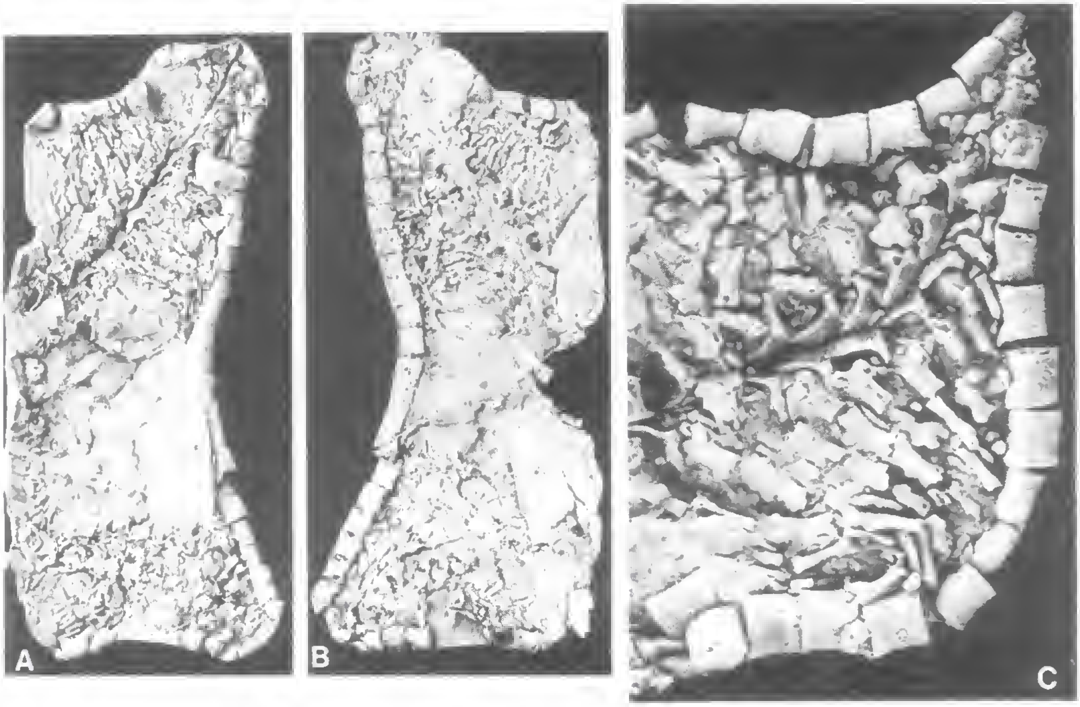


FIG. 43. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia. A,B, NM 39/83, fully articulated specimen showing the interradial gap in plating, x2. A, oral surface. B, aboral surface. C, NM L10069, one arm showing ambulacrals, adjacent adambulacrals and complex interradial plating, x5.5. Latex casts whitened with ammonium chloride sublimate.

The second ambulacral plate is slightly pinched about one third of the distance from the proximal end (Fig. 47B, C). It carries two half podial basins on its perradial side separated by an oblique ridge. The smaller proximal basin faces laterally while the larger distal basin faces more adorally. The proximal half podial basin fits against the half podial basin on the distal end of the first ambulacral to create a completely enclosed basin. There is a broad distal tongue that imbricates with the third ambulacral plate. The interradial face is smooth and cylindrical. There is a small lateral arm plate that attaches to the transverse bar.

The third ambulacral plate resembles more distal ambulacral plates except that it has a much larger proximal end with a prominent raised rim abradially marking the limit of overlap of the second ambulacral plate (Fig. 47C, D).

Madreporite and stone canal. The madreporite is seen in a number of specimens (Figs 37A, 38B, 39B,C, 41D). It is a large button-shaped ossicle, circular in outline, situated in one of the interrays close to the mouth. Because the madreporite is not part of a tesselate surface and has often collapsed after death, Spencer (1951) was not sure whether it was aboral or oral in position. However, 11 specimens in which the madreporite can be seen show the central part of the disc with ambulacra undistorted and all five ambulacra facing the same direction. In all 11 specimens the madreporite lies with its outer surface facing aborally and so we conclude that the madreporite lay on the aboral surface. The outer face of the madreporite is ornamented with a series of branching grooves radiating from the centre (Fig. 48A). The inner face is more domed and is smooth (Fig. 48B). Towards the centre there is a scroll- shaped perforation which marks the site of attachment for the stone canal.

The stone canal is best seen in NM L10150 and L10438, but is present in other specimens also. It is a tube built up of a single series of stacked cylindrical ossicles. These ossicles are oval in outline and show a U-shaped outer calcitic sheath surrounding an anchor-shaped core (Fig.

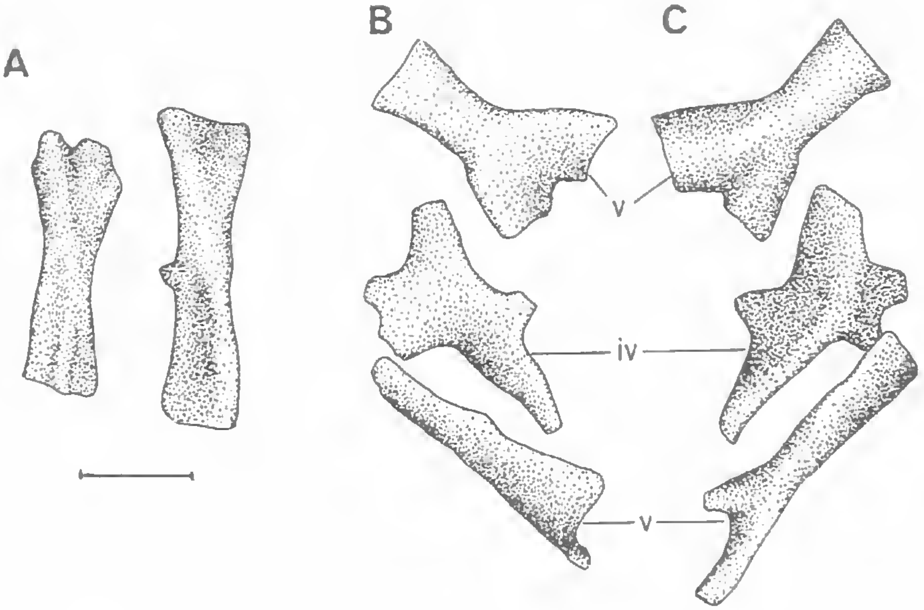


FIG. 44. *Archegonaster pentagonus* Spencer. Llanvirn of Osek, Czechoslovakia, camera lucida drawings of interradial elements; A, NM L10438, two first virgals. B, NM L10457, two first virgals (v) and an intervirgal (iv) in part and counterpart view. Scalebar = 1 mm:all to same scale.

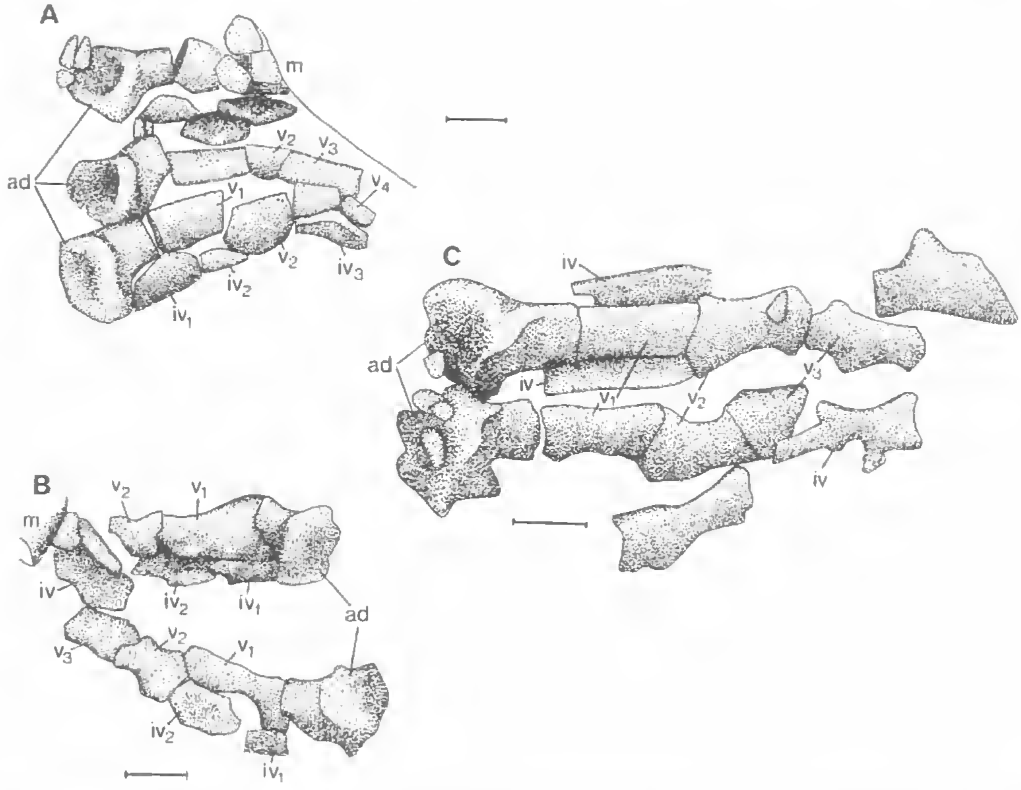


FIG. 45. *Archegonaster pentagonus* Spencer. Llanvirn of Osek, Czechoslovakia, camera lucida drawings of interradial plating. A, NM 43/83. B, NM L10446. C, NM L43183. ad = adambulacral plate. v_1, v_2, v_3, = first second and third virgal plates. iv = intervirgal plate. m = marginal. Scale bar = 1 mm.

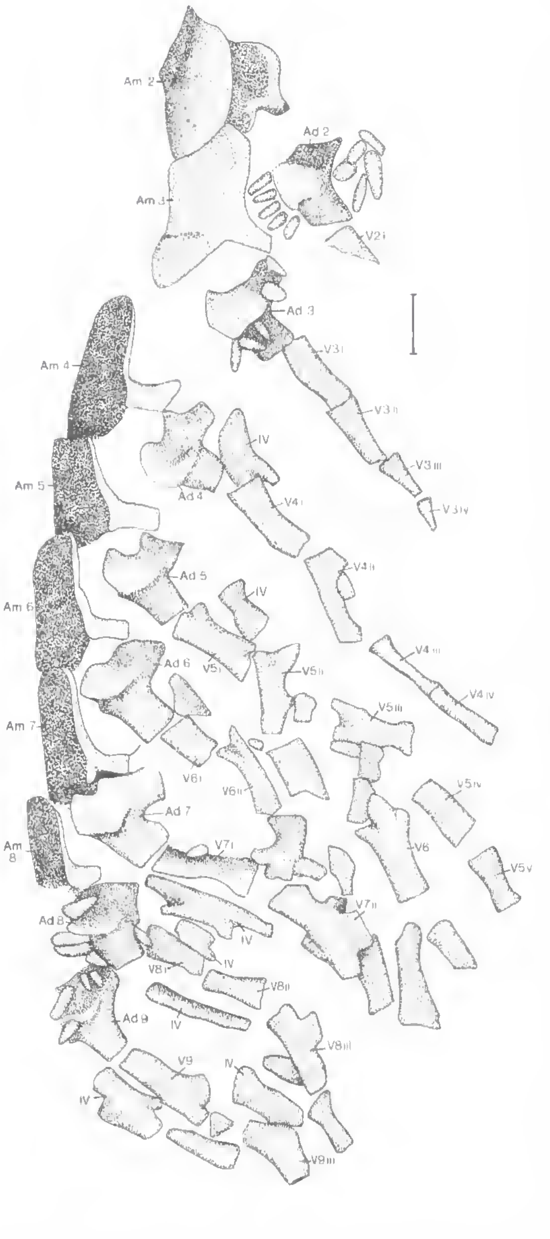


FIG. 46. *Archegonaster pentagonus* Spencer, NM L10450, Llanvirn of Osek, Czechoslovakia, camera lucida drawing of one half of an arm from the second ambulacral to the ninth showing relatively undisrupted interradial plate arrangement. am2-8 = ambulacrals 2 to 8. ad2-9 = adambulacrals 2 to 9. V2-9 = virgals forming row from adambulacrals 2 to 9 (successive virgals are labelled as i, ii, iii, iv, v). IV = intervirgal plates.

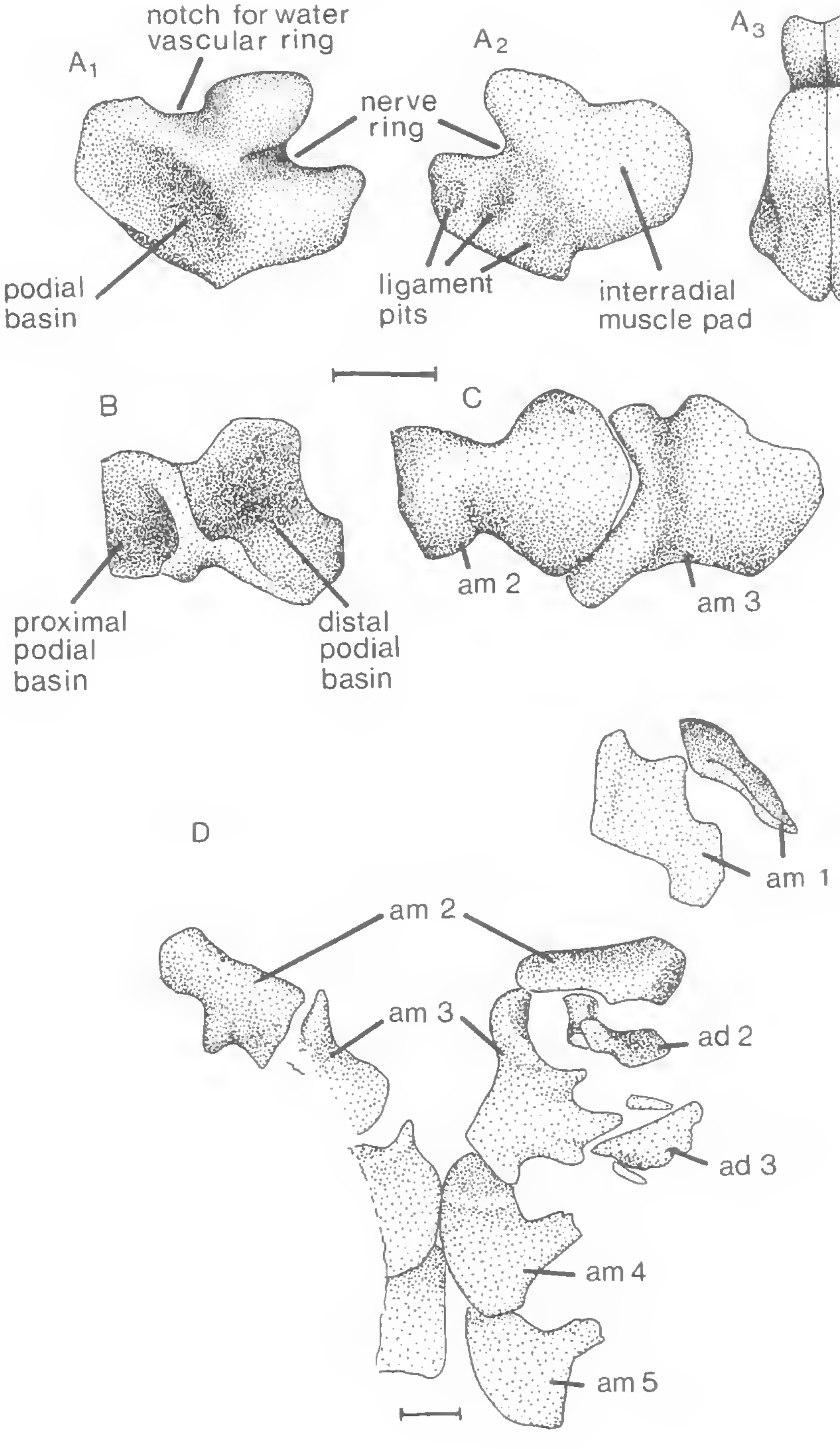
48C). A scroll-shaped cavity runs through each ossicle.

Marginals. The complete rim of stout marginal ossicles (Figs 37, 38) is formed by cylindrical ossicles that abut along smooth, slightly concave lateral faces (Fig. 50). Three specimens of disarticulated *Archegonaster* plates from a slightly higher horizon (D γ2 of Zbytky hvesdic, Šarka) have a crenulate rim to the lateral faces of marginal ossicles and may represent a separate species. The marginals are largest interradially and decrease in size towards the arm tips (Fig. 49A,D). They are slightly triangular in cross-section, with the two longer and slightly flatter faces being the external aboral and oral faces. These faces, in large ossicles, have a narrow smooth border and bear a distinct, but fine, pitted ornament (Figs 49A, 50). The inner face is more rounded and lacks the pitted ornamentation. There is a distinct ledge on the aboral face marking the boundary between inner and outer faces. Some ossicles are distinctly saddle-shaped. The inner face usually has small projecting facets that are rounded or vertically elongate (Figs 38E, 43C, 50). There is usually a single facet to each marginal ossicle, but occasional ossicles may bear two. The most interradial 5 or so ossicles lack facets (Fig. 49A). These facets are the attachment points for the interambulacral skeleton.

The 17-27 marginal ossicles from the interradius to the arm tip, indicate that there were some 170-270 marginal ossicles in the complete ring. The marginals diminish in size markedly towards the tips of the arms, where they become almost U-shaped in cross- section with a slightly concave inner face. In the outer part of the arm the marginals sheath the ambulacral groove (Figs 49B,C, 50D).

Aboral surface. Aboral plating is composed of small (c. 0.05 mm diameter) granular plates, closely packed together. In one specimen this tegmen coats the entire surface and is wrinkled, showing that it was flexible (Fig. 49C). It ends at the small ledge on the aboral face of marginal

FIG. 47. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia, camera lucida drawings of proximal ambulacral plating. A, first ambulacral (= mouth angle plate). A_1, perradial face. A_2, interradial face. A_3, aboral face (two adjacent plates abutting, slightly restored) drawn from NM L10149 and L10150). B, second ambulacral plate in perradial view (NM L10476). C, second and third ambulacrals in interradial view (NM 41/83). D, proximal ambulacral plates in NM EH30, plating slightly disrupted. Scale bars = 1 mm.


A1
notch for water vascular ring
nerve ring
podial basin
A2
ligament pits
interradial muscle pad
A3
B
proximal podial basin
distal podial basin
C
am 2
am 3
D
am 1
am 2
am 3
ad 2
ad 3
am 4
am 5

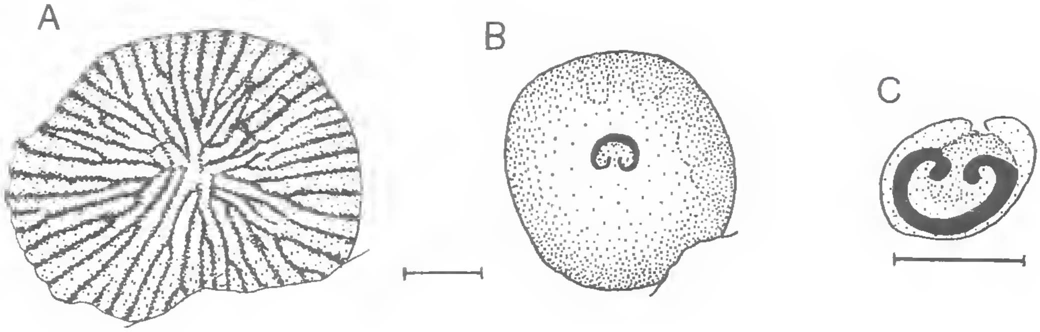


FIG. 48. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia, camera lucida drawings. A, exterior of madreporite plate (NM L10434). B, interior of madreporite plate: note the scroll-shaped perforation (NM L10444). C, end view of a single barrel-shaped ossicle of the stone canal (NM L10438). Scale bar = 1 mm.

ossicles marking the boundary between the pitted ornament of the external surface and the smooth internal surface.

REMARKS

Archegonaster was described by Spencer (1951) but, because all the material was preserved as moulds and high quality latex casts were unavailable to Spencer, the description is inadequate in many respects. Spencer, for example, believed that the virgals formed a single series and that they were developed only towards the arm tips.

Archegonaster is considerably derived in comparison to any known Cambrian echinoderm and shows several characteristics that link it to ophiuroids and asteroids in particular. There is a madreporite and stone canal. The aboral position of this madreporite suggests that *Archegonaster* lived with its mouth facing the substratum, since the madreporite would need to be clear of sediment to function efficiently. It also has adambulacrals that articulate onto transverse bars from the ambulacrals and which carry spines. The most proximal ambulacral plates are modified into a jaw and the ambulacral tips extend outwards as arms, though still bound within the marginal frame.

However, it remains relatively primitive in comparison to ophiuroids. The radial water vessel is not enclosed and the ambulacral plates, at least proximally, are strongly imbricate. The adambulacrals attach directly to the marginals or via a series of interradial plates and the oral surface is bounded by a well-developed marginal frame. Spencer (1951) believed that *Archegonaster* was the most derived of his somasteroids (largely because it was slightly younger than *Villebrunaster* and *Chinianaster*), but both *Villebrunaster* and *Chinianaster* have enclosed radial water vessels and reduced marginal ossicles and are thus morphologically closer to ophiuroids than *Archegonaster*. The plate arrangement towards the tips of the arms of *Archegonaster* resembles that of asteroids, with the adambulacrals attaching directly on to the marginals, both marginals and adambulacrals being stout, block-like ossicles.

The imbricate ambulacrals are peculiar; no Cambrian edrioasteroid has such strongly imbricate plating, although limited imbrication is present in all. Nor do any of the Ordovician asteroids or ophiuroids have a comparable arrangement. However, the ambulacral plates towards the arm tip in *Archegonaster* strongly resemble ambulacral plates in Cambrian edrioasteroids such as *Cambraster walcotti* (Smith, 1986, text-fig.7). Imbrication is best developed towards the mouth and is least developed towards the arm tips, thus allowing greatest flexibility of shape towards the centre of the disc. This may be associated with the adoption of a macrophagous diet.

Mouth frame plating. The structure of the ambulacra closest to the mouth is particularly revealing when considering the origins and homologies of the ophiuroid jaw. However, conflicting nomenclature and concepts of homology are to be found in the literature and it seems

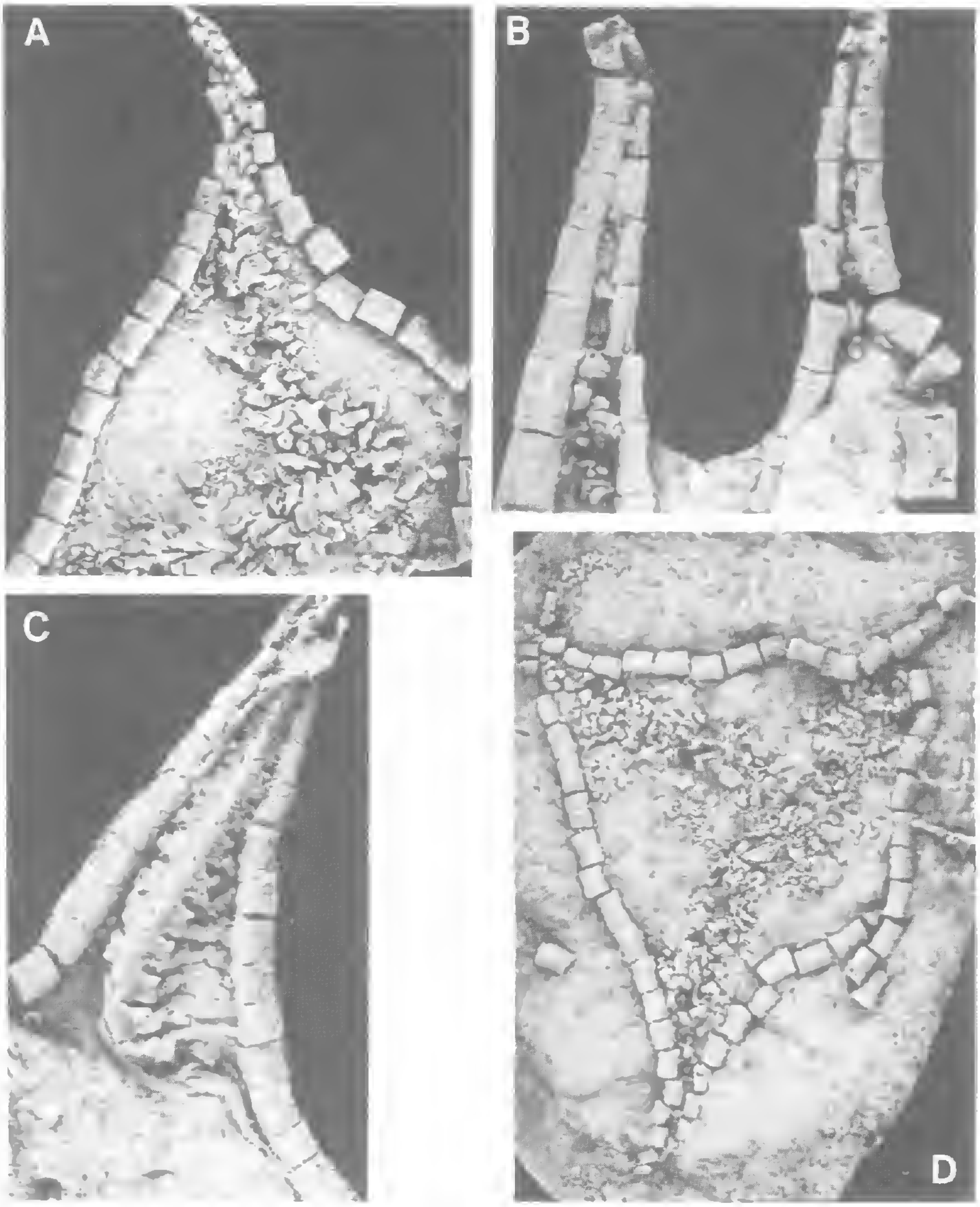


FIG. 49. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia. A, NM L25172, one arm in aboral aspect, x3. B, NM L10462, two arms towards their tips in oral aspect, x8. C, NM L35050, one arm in aboral aspect, x5: note the aboral integument of granules which is wrinkled towards the base of the arm. D, unnumbered specimen in the Narodní Museum showing the tapering arms; note that the disc is folded over upon itself, x2.5.

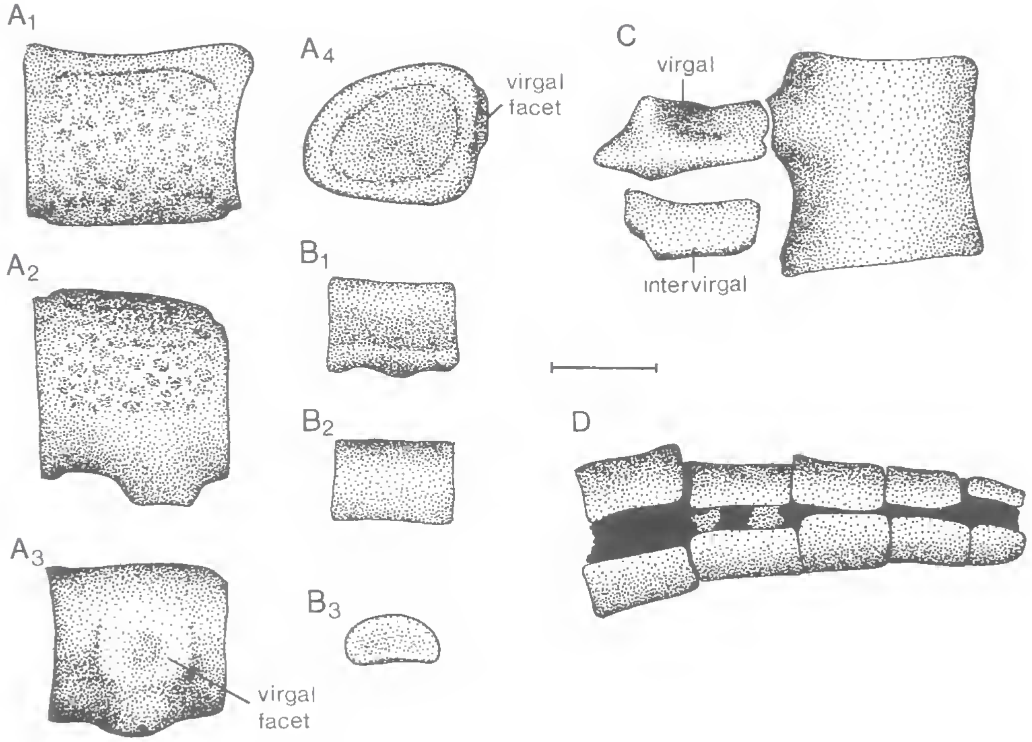


FIG. 50. *Archegonaster pentagonus* Spencer, Llanvirn of Osek, Czechoslovakia, camera lucida drawings of marginal ossicles. A_{1-4}, Aboral, oral, internal and lateral aspects of a large marginal of the central part of the disc (drawn from NM L10150, L13228 and L10438). B_{1-3}, internal, external and lateral aspects of a marginal towards the arm tips (drawn from NM L10462). C, marginal with virgal attached (NM L13228). D, distal tip of an arm in oral aspect showing how the marginals protect the ambulacral groove (NM L10462). Scale bar = 1 mm.

advisable to correct this in the interests of uniformity for future descriptions.

Spencer (1914, p. 29; 1925, p. 263) believed that the most proximal set of 10 plates in the ophiuroid mouth frame were interradial in origin and therefore modified interambulacral plates rather than ambulacral plates. These most proximal elements he named 'mouth angle plates'. In his scheme the second plates of the ophiuroid jaw, distal to each mouth angle plate were the first of the ambulacral plates and, accordingly, he termed these plates 'ambulacral 1'. This nomenclature has been followed by many subsequent authors and was reinforced in the *Treatise* by Spencer & Wright (1966), despite their acknowledgement (Spencer & Wright 1966, pp. 13,14,29) that the mouth angle plate is part of the ambulacral series. Fell (1963) affirmed the ambulacral origin of the mouth angle plates and Bjork *et al.* (1968) went so far as to denote the plate behind the mouth angle plate (which Spencer (1925) and Spencer & Wright (1966) referred to as ambulacral 1) as ambulacral 2. However, Kesling & Vasseur (1971, fig. 8) reverted to Spencer's terminology, and the *Treatise* terminology (Spencer & Wright, 1966) has become standard over the last 20 years.

Such terminology contradicts the origins and homology of the mouth plates and ought to be abandoned. We therefore advocate, and henceforth use, the following set of terms: the most proximal plate of each ambulacral column, situated interradially will be the 'first ambulacral' or 'mouth angle plate'; the succeeding plate is the 'second ambulacral' and subsequent ambulacral plates are denoted accordingly as ambulacrals 3, 4, etc.

The first ambulacral bears the anterior half of a podial basin in *Archegonaster* (Fig. 47) and a slight depression from the aboral water vascular ring canal marks the position of the lateral branch leading to this podial basin. We interpret this groove as the site of a branch of the water vascular system leading to the first tube foot in that podial basin. The position of this branch leaves it vulnerable to damage from larger particles that were ingested. Evolution led to enclosure of that branch of the water vascular system, giving greater protection, and this condition is found in most subsequent ophiuroids. Similar enclosure of a canal in the second ambulacral would lead to the arrangement that is found in *Lapworthura miltoni* (Salter), for example (Spencer, 1925, fig. 191). Likewise in each arm segment the passage connecting each podial basin with the radial water vessel, which in *Archegonaster* appears as a notch, is ultimately enclosed within the ambulacral plate. In *Lapworthura* the opening of the canal leading from the water vascular canal to the first podial basin has shifted onto the second ambulacral and thus pierces through two plates. As the first and second ambulacrals are closely fixed together, passage of this canal from one plate into the other would pose little problem. The situation in post-Palaeozoic ophiuroids and in Palaeozoic euryalinids is for there to be a single aboral pore in ambulacral two which divides internally to feed both the first and second podial basins. This is a derived condition and cannot be used to argue that the second ambulacral plate is a compound plate, as has been done by Bjork *et al.* (1968). The general one to one correspondence of podial basins to ambulacrals and adambulacrals to ambulacrals in early forms such as *Archegonaster*, *Eophiura* (pers. obs.; Spencer & Wright, 1966, fig. 70-1), and *Praedesura* (pers. obs.; Spencer & Wright, 1966, fig. 23-3) among others, gives us confidence that no ambulacrals are compound plates. Only one element has not been identified in these early forms and that is the adambulacral element of the first ambulacral. We believe that the torus that abuts the proximal end of ambulacral 1 represents the modified adambulacral 1. On this interpretation the spines on the torus would be the modified lateral spines of the adambulacral. It is not difficult to envisage the most proximal adambulacrals in primitive members becoming modified for food manipulation in the same way that the proximal tube feet became modified into buccal tentacles. Although most ophiuroids have 5 torus plates, one for each pair of interradially joined first ambulacrals, several do have 10 plates, one for each first ambulacral (e.g. Spencer, 1925, fig. 188C). Although the situation in *Archegonaster* remains unclear, we believe that the primitive condition is for there to be ten torus plates bearing mouth spines.

Structural and functional specialization of the more proximal elements around the mouth were undoubtedly associated with the change from suspension to deposit feeding. In suspension feeding a fixed mouth frame gives strength and rigidity, but for deposit feeding flexibility of the mouth is essential. The proximal ambulacrals thus became very different in appearance to more distal arm plates. Significantly the homologies that we propose allow for the development of the ophiuroid jaw from the simple ambulacral and adambulacral series through only a few steps, each relating to specific functional needs. We do not need to invoke the loss or gain of any plate, nor any compounding of plates. Furthermore it gains support from the most recent embryological work of Hendler (1978) who has also argued for the ambulacral origin of the mouth angle plates in living ophiuroids.

The most proximal elements (ambulacra 1) are highly modified in shape and carry a groove for the circum-oesophageal ring nerve and water vascular ring. Their general shape and soft tissue associations leave no doubt that they are homologous to the mouth angle plates of ophiuroids. In *Archegonaster* these plates are in direct continuity with other ambulacrals and carry a partial podial basin towards the posterior which is shared with the next ambulacral plate. Spencer (1925) thought that the first plates in the ophiuroid jaw were modified adambulacrals, since the first podial basin is found on the second of the jaw plates and the adambulacrals are in direct alignment with the first jaw plates (mouth angle plates). That the mouth angle plates cannot be modified adambulacrals of the so-called 'first ambulacrals' is further reinforced by the fact that these plates bear a small adambulacral in *Archegonaster* discrete from the mouth angle plates.

Mouth angle plates of *Archegonaster* are similar to those of primitive ophiuroids such as *Eophiura* in lying in the same plane as the rest of the ambulacrals. In later ophiuroids the second ambulacral plates are highly modified and project aborally over the third ambulacrals. However, the basic pattern of having the first ambulacral plates interradial in position and the second ambulacral plates set oblique to both the proximal elements and the rest of the ambulacra, is common to both *Archegonaster* and all ophiuroids.

The connection between *Archegonaster* and asteroids is less clear-cut. Unquestionable Ordovician asteroids (viz. *Platanaster*) differ from *Archegonaster* in having block-like ambulacrals that firmly abut, but have a comparable arrangement of plates around the mouth. As noted above, the ossicles become much more block-like distally along the arms in *Archegonaster* and the radial water vessel is not enclosed, as in all asteroids. The marginal ossicles are probably directly homologous with the marginals or submarginals of Ordovician asteroids, and forms such as *Petraster* have prominent block-like marginals framing the oral face.

Antecedents of *Archegonaster* are still unclear. Although *Archegonaster* is morphologically primitive in comparison to asteroids and ophiuroids considerable differences remain between it and any known edrioasteroid. However, despite the limited evidence with which to trace the Cambrian antecedents of *Archegonaster*, we take the pragmatic view that, amongst known forms, every taxon has another that is its closest known relative. The stout marginal ring framing the body and the projection of ambulacral tips onto the marginal ring of *Archegonaster* are suggestive of either *Cambraster* or *Edriodiscus*. However, both of these genera have a peripheral skirt of platelets and an oral periproct, neither of which is found in *Archegonaster*. The mouth plating in *Archegonaster* was flexible and presumably under muscular control, whereas *Cambraster* has a fixed mouth frame of 5 large interradial elements that represent fused first ambulacral plates from adjacent ambulacra. The mouth frame of *Edriodiscus* is unknown, but externally resembles that of *Stromatocystites* which consists of the 10 most proximal ambulacral plates (Smith, 1986). Since we do not believe that the flexible mouth plating of *Archegonaster*, comprising the most proximal 10 ambulacral ossicles, is likely to be derived from a form in which proximal ambulacrals have become fused and modified into 5 large interradial elements, a Cambrian edrioasteroid with unfused proximal ambulacrals seems the most plausible antecedent to *Archegonaster* and its descendents. Thus current evidence points to *Edriodiscus* as the closest known relative of *Archegonaster* amongst Cambrian echinoderms. We predict that further intermediates between edrioasteroids and *Archegonaster* will be found in the Middle and Late Cambrian.

GENERAL DISCUSSION

PHYLOGENY

There are five principal echinoderm groups in the Ordovician whose ancestry lies in the Cambrian edrioasteroids, namely edrioasterids, isorophids, rhenopyrgids plus cyathocystids, edrioblastoids and *Archegonaster* and its derivatives (including both asteroids and ophiuroids). Smith (1986) presented a cladistic analysis of a number of these groups but specifically excluded *Archegonaster* and its relatives, which had not at that point been studied. In this paper we have accumulated more evidence about the morphology of primitive edrioasteroids and added a number of new taxa, as well as documenting the morphology of *Archegonaster*. It is therefore appropriate to reanalyse edrioasteroid relationships in the light of this new information.

A data matrix was assembled (Fig. 51; Table 1) based on as much morphological information as is currently available. This was then subjected to a computer parsimony analysis using Hennig86 (Farris, 1988). All characters were treated as unordered and *Camptostroma* was used to root the tree. A total of 108 equally parsimonious trees were found of length 32 and consistency index 62 (Fig. 51).

Stratigraphical occurrence data for relevant early Palaeozoic eleutherozoan taxa (Fig. 52) include all Cambrian edrioasteroids and the earliest occurrences of all major post-Cambrian eleutherozoan lineages. By combining the cladistic analysis with stratigraphical data we arrive at the best corroborated evolutionary tree (Fig. 53).

The origins of edrioasteroids may be traced back to the recently described late pre-Cambrian *Arkarua* (Gehling, 1988) from the Pound Subgroup (Rawnsley Quartzite) of South Australia. *Arkarua* is still poorly known, and we do not even know whether it had a blind gut or an anus. However, it shows more resemblance to Cambrian edrioasteroids than to any known ediacaran species and we tentatively accept it as an early echinoderm and the oldest known pentaradiate species. The Cambrian fauna is better known and Paul & Smith (1984) suggested that *Camptostroma* represented an intermediate stage bridging the morphological gap between pelmatozoans such as *Kinzercystis* and eleutherozoans such as *Stromatocystites*. Pelmatozoans and eleutherozoans were already differentiated by the late Lower Cambrian.

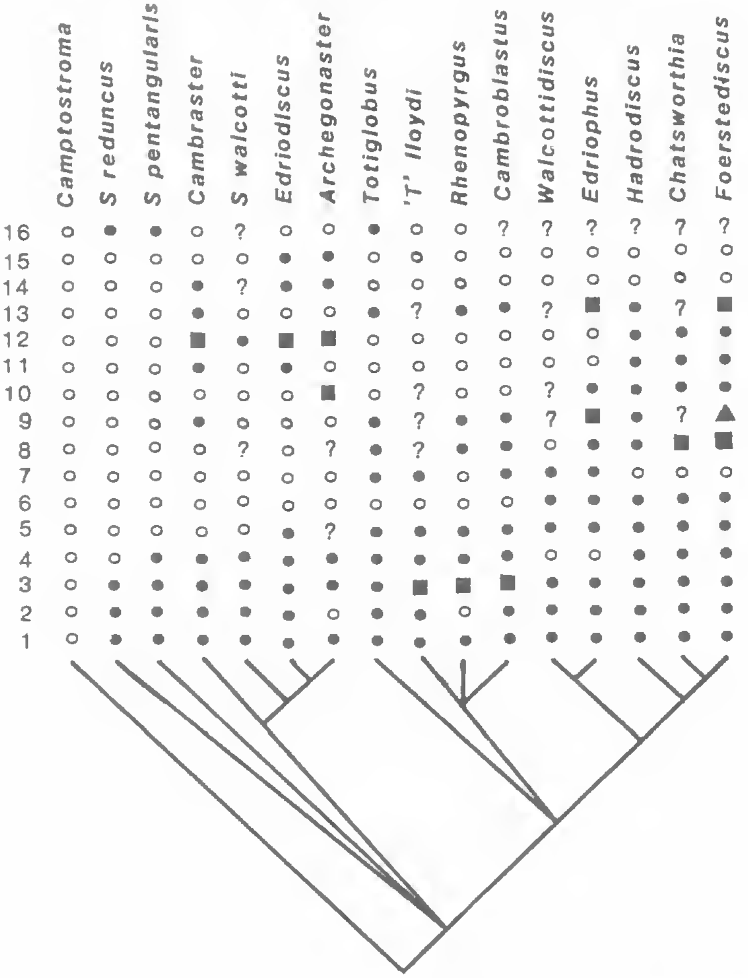
Our cladistic analysis suggests that *Stromatocystites* represents a generalised eleutherozoan and that the origins of later eleutherozoan groups can be traced back to it. There are several species currently included in the genus which is probably paraphyletic. We recognise two distinct lineages originating within *Stromatocystites*. From *S. pentangularis* one lineage gave rise to *Totiglobus*. *Totiglobus* has internal struts on aboral plates that Bell & Sprinkle (1978) interpreted as an attachment device. Such struts are also found in *Stromatocystites pentangularis* and *S. reduncus*, where they are better developed. Two important differences distinguish *Totiglobus* from *Stromatocystites*, the structure of the oral frame and the enlargement of the oral surface relative to the aboral surface. Whereas *Stromatocystites* has an oral frame formed from the 10 most proximal ambulacral ossicles *Totiglobus* and its relatives have an oral frame of 5 large interradial elements. This character is also seen in the Late Cambrian edrioblastoid *Cambroblastus* as well as in the Ordovician and younger Cyathocystida (i.e. Cyathocystidae and Rhenopyrgidae). The late Middle Cambrian *'Totiglobus' lloydi* Sprinkle (1985) has a similarly shaped theca but the aboral portion of the theca appears in side view and, although broken off, could be interpreted as forming a short peduncle of sub-tesselate plates. In the slightly younger *Cambroblastus* the aboral surface has been greatly expanded into a polyplated stalk and this lineage continued into the Ordovician to give rise to the edrioblastoid *Astrocystites*. *Cambroblastus* is essentially the body of *Totiglobus* raised on a stalk.

Because cyathocystids have an elongate, stalk-like aboral surface and because they have reduced their flooring plates to a single large deltoid lying interradially (Bockelie & Paul, 1983), we believe that they represent a sister group to *Cambroblastus* and later edrioblastoids. Rhenopyrgids probably have a similar reduction in ambulacral flooring plates, to judge from external plating, but the precise arrangement has never been described. They differ from cyathocystids in having a polyplated, imbricate aboral surface rather than a single massive turret that is a single calcite crystal. We therefore agree with Bell (1980) and Bockelie & Paul (1983) in suggesting that cyathocystids represent a distinct line of descent from isorophids and edrioasterids, and are more closely related to edrioblastoids. However, we also include rhenopyrgids within this group because of their aboral stalk pending confirmation of their ambulacral flooring plate arrangement.

Another group with an aboral attachment disc and with an expanded oral surface relative to the aboral surface includes *Walcottidiscus* and its descendents the edrioasterids. These we believe represent a separate line of descent from a *Totiglobus*-like ancestor. In this lineage the aboral surface became uncalcified. The origin of isorophids remains problematic, but *Hadrodiscus* may represent an intermediate morphology between edrioasterid-like forms and later isorophids. *Hadrodiscus* still retains large deltoid-like oral frame plates that lie interradially and may have had biserial flooring plates, although in external appearance it has a peripheral rim and the flattened streamlined appearance of an isorophid. The peripheral rim plates in isorophids appear not to be homologous with the peripheral ring in forms such as *Edriodiscus*, to judge from the cladistic analysis. They certainly appear rather different; in *Edriodiscus* the marginals are stout, barrel-shaped ossicles that abut, whereas in isorophids the marginals are thin imbricate plates that overlap. However, there remains the possibility that isorophids were derived from a more disc-like form such as *Cambraster*.

Stromatocystites walcotti, from the Lower Cambrian, appears different from other *Stromatocystites* spp. in being flat and disc-like, with slightly differentiated marginal ossicles. This disc-like form and rather flat, simple ambulacral ossicles are also seen in the early Middle Cambrian *Edriodiscus*. As argued above, we believe that *Edriodiscus* is the sister group to *Archegonaster* and thus a possible precursor to the major post-Cambrian eleutherozoan groups of asteroids and ophiuroids.

The position of *Cambraster* is problematic because it shows a mixture of characteristics. On the one hand it has an oral frame composed of 5 large interradially positioned flooring plates (Smith, 1986) which link it to the *Totiglobus* group. On the other hand it has a virtually identical peripheral ring and body form to *Edriodis-*



	Camptostroma	*S reduncus*	*S pentangularis*	*Cambraster*	*S walcotti*	*Edriodiscus*	*Archegonaster*	*Totiglobus*	*'T' lloydi*	*Rhenopyrgus*	*Cambroblastus*	*Walcottidiscus*	*Edriophus*	*Hadrodiscus*	*Chatsworthia*	*Foerstediscus*
16	○	●	●	○	?	○	○	●	○	○	?	?	?	?	?	?
15	○	○	○	○	○	●	●	○	○	○	○	○	○	○	○	○
14	○	○	○	●	?	●	●	○	○	○	○	○	○	○	○	○
13	○	○	○	●	○	○	○	●	?	●	●	?	■	●	?	■
12	○	○	○	■	●	■	■	○	○	○	○	○	○	●	●	●
11	○	○	○	●	○	●	○	○	○	○	○	○	○	●	●	●
10	○	○	○	○	○	○	■	○	?	○	○	?	●	●	●	●
9	○	○	○	●	○	○	○	●	?	●	●	?	■	●	?	▲
8	○	○	○	○	?	○	?	●	?	●	●	○	●	●	■	■
7	○	○	○	○	○	○	○	●	●	○	●	●	●	○	○	○
6	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●
5	○	○	○	○	○	●	?	●	●	●	●	●	●	●	●	●
4	○	○	●	●	●	●	●	●	●	●	●	○	○	●	●	●
3	○	●	●	●	●	●	●	●	■	■	■	●	●	●	●	●
2	○	●	●	●	●	●	○	●	●	○	●	●	●	●	●	●
1	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●

FIG. 51. Character matrix and cladogram for Cambrian edrioasteroids and related taxa. Characters 1-16 are listed in Table 1. symbols are as follows:- open circles = plesiomorphic state. solid symbols = derived state (circles, squares and triangles indicate different character states). ? = character state unknown.

cus. For the moment we have accepted its placement as shown in the cladogram (Fig. 51), pending further information.

ECOLOGICAL DIVERSIFICATION

Having examined the phylogenetic relationships of the major edrioasteroid groups we can now consider the palaeobiological significance of the various evolutionary changes that occurred. We trace edrioasteroids back to the Lower Cambrian *Camptostroma*, which lies close to the latest common ancestor of pelmatozoan and eleutherozoan echinoderms (Paul & Smith, 1984, Smith,1988b). *Camptostroma* has a broad, conical aboral surface that was contractile and it lived with its pointed base inserted into unconsolidated sediment. It was a sedentary suspension feeder using its curved ambulacra to collect food particles which were then passed to the mouth along the food grooves.

Most later groups specialised for attachment to firm or hard substrata and were thus able to colonize higher energy environments and presumably gained access to a richer food source. The evolution of attachment in edrioasteroids is thus seen as a direct adaptation for resisting dislodgement in currents. The earliest forms (*Stromatocystites*) retained a fully plated aboral surface which was modified into an attachment pad. They were certainly not permanently attached to a substratum but probably used their aboral surface to adhere to firm sedimentary bottoms. No *Stromatocystites* is known to be attached to any form of hard substratum, such as a shell and they appear to have been low level suspension feeders living in

Primitive	Derived
1. Thecal plating multilayered Thecal plating	1 layer only
2. Imbricate aboral plating	Aboral plating a tesselate pavement
3. Conical base	(●) flat (■) aboral stalk
4. Ambulacra curved	Ambulacra straight
5. Epispires present	Epispires lost
6. Aboral surface fully plated	Aboral surface partially or completely uncalcified
7. Oral surface weakly domed	Oral surface strongly inflated
8. Cover plates a multiplated skirt	(●) Cover plates of large primaries plus small secondaries (■) Cover plates large, with intrathecal portion
9. Mouth frame of 10 ambulacral plates	Mouth frame of (●) five fused interradially positioned elements (■) five radial elements that are not flooring plates. (▲)five uniserial flooring plates
10. Anal opening a cone of lath-shaped plates	(●)Anal opening a periproct of small platelets (■)anal opening aboral or lost
11. No peripheral rim of plates	Peripheral rim plates
12. Marginals absent	(●) marginal ring of large imbricate plates (■) marginal ring of stout block-like ossicles
13. Flooring plates of *S. pentangularis* type	Flooring plates of (●) *S. walcotti* type (■) isorophid type.
14. Ambulacra restricted to oral surface	Ambulacra extend through marginal rim
15. Marginals	Marginals intergral part of both oral and aboral surfaces.
16. No internal ribbing on aboral surface	Internal ribbing developed

TABLE 1. Characters used in the phylogenetic analysis of early Palaeozoic eleutherozoans (autapomorphies ommitted).

moderately protected environments. Edrioasterids, from *Walcottidiscus* onwards, continued in this mode of life but became uncalcified over the central part of their aboral surface, presumably to improve adhesion.

From this basic attachment style there developed 4 specialised offshoots. Firstly, *Totiglobus* evolved towards becoming a higher level suspension feeder by reducing its aboral attachment pad and expanding its oral, food-gathering area into a globular surface. Attachment remained identical to that in *Stromatocystites* and we do not believe that *Totiglobus* was capable of resisting strong currents. Secondly, isorophids became much more streamlined in profile, with a well-developed peripheral rim of plates to strengthen the theca. Isorophids have completely uncalcified aboral surfaces and are generally found attached to hardgrounds or shells. They thus lived limpet-like in areas of relatively strong current activity and were able to invade many shallow water habitats previously unavailable to edrioasteroids. Thirdly, cyathocystids evolved even more secure attachment by cementing themselves to hardgrounds. Their entire aboral surface became a single cal-

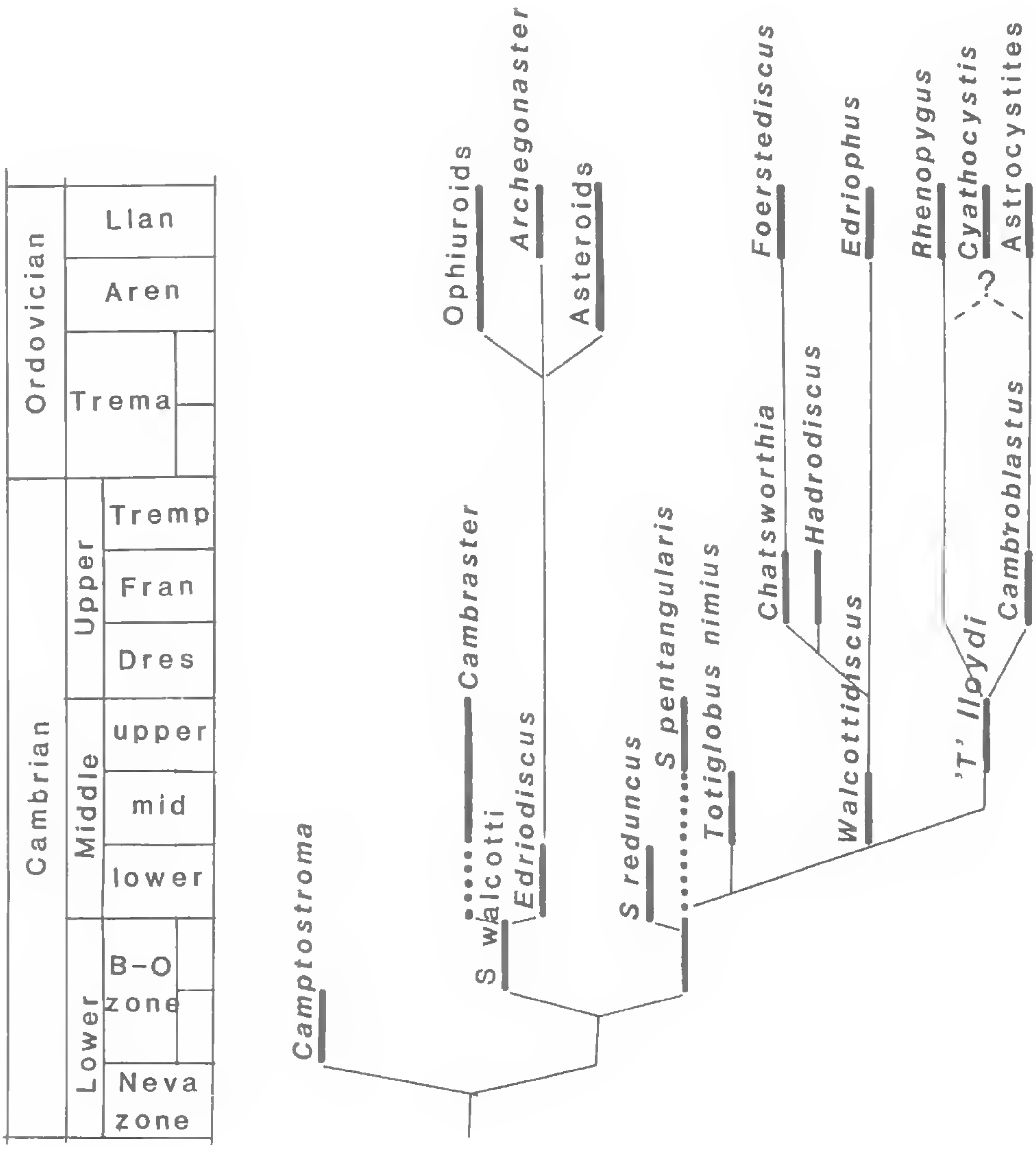


FIG. 52. Stratigraphical range chart for early Palaeozoic edrioasteroids and related taxa. Heavy lines = known stratigraphical range. thin lines show implied evolutionary relationships.

cite tube which was firmly attached to a hard substratum such as a shell. These forms must have been particularly well adapted for life in high energy regimes. Fourthly edrioblastoids also evolved an aboral attachment disc and fixed to hard substrata, though precisely how is still unknown. Their aboral surface became transformed into a stiff stalk which elevated the food gathering area well above the substratum and they represent the only edrioasteroids to become relatively high-level suspension feeders. Presumably they were adapted for habitats of intermediate current strengths.

Two edrioasteroid lineages departed from the attached mode of life to gain access to different habitats. Rhenopyrgids became infaunal suspen-

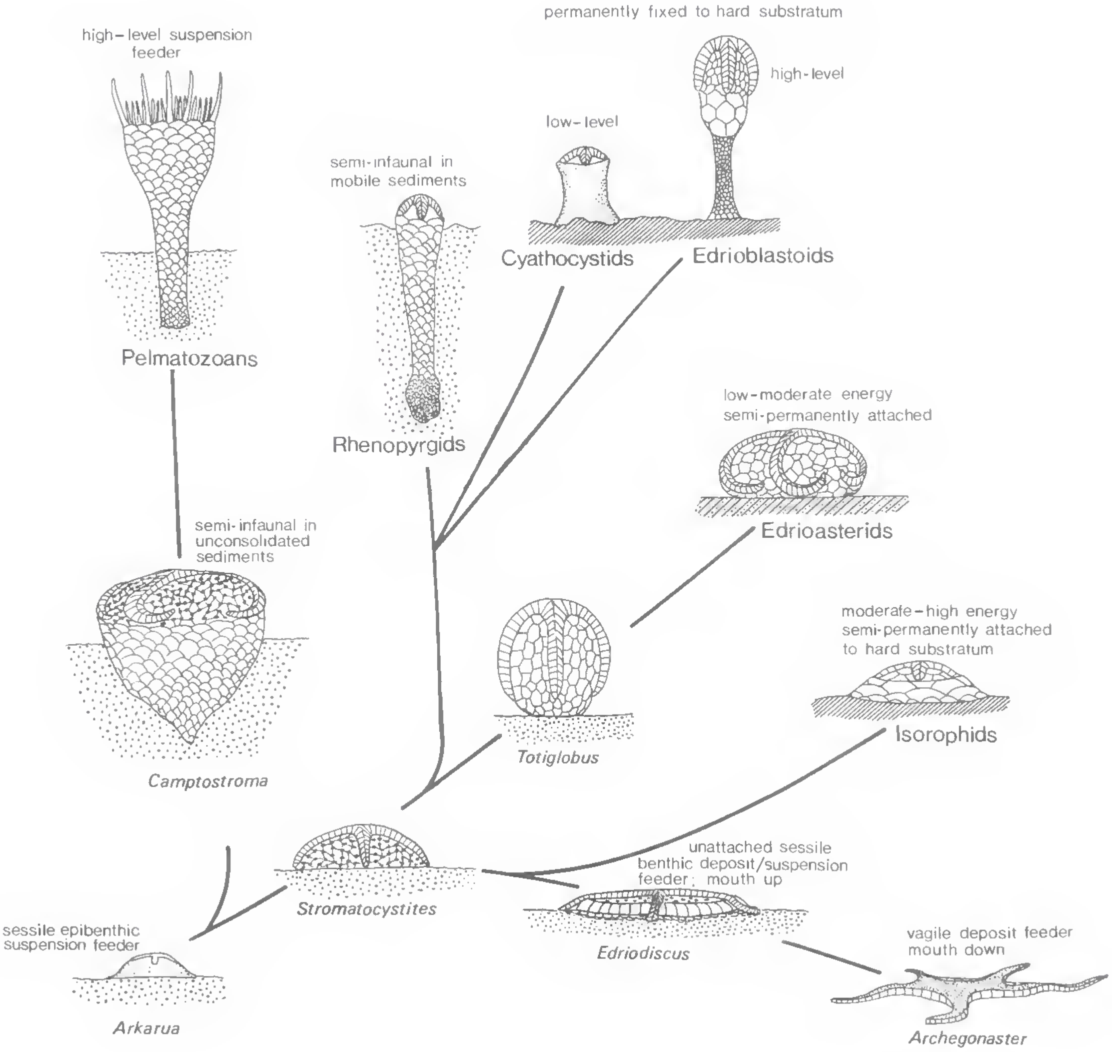


FIG. 53. Ecological diversification of early Palaeozoic eleutherozoans.

sion feeders in mobile, unconsolidated sediments. Their aboral surface is modified into a long, flexible and highly extensible peduncle which terminates in a basal sac. This peduncle we believe was inserted into the sediment so that rhenopyrgids were firmly anchored. The peduncle could then be used to retract the animal into its burrow, in an analogous way to the brachiopod *Lingula*, and was presumably adapted for life in more mobile sedimentary substrata.

The other lineage to depart from attachment includes the flattened disc-like forms *Cambraster* and *Edriodiscus*. Both either lost, or never evolved, an aboral attachment disc and have simple aboral plating instead. They presumably were low level suspension feeders in protected habitats where attachment was unnecessary. Both have a stout marginal frame to strengthen the body. This line we believe gave rise through inversion to the free-living forms such as *Archegonaster* which were deposit feeders living with their oral surface towards the substratum. From them evolved the asteroids and the opuroids.

THE CAMBRIAN DIVERSIFICATION

As noted in the introduction, there are two contrasting explanations as to why Upper Cambrian echinoderms are uncommon. One explanation is that evolutionary diversification occurred in two phases, the first in the Lower and Middle Cambrian and the second in the Ordovician (Sprinkle, 1980a, 1981; Campbell & Marshall, 1987). The alternative explanation is that diversification was continuous throughout this period but that Upper Cambrian faunas were rarely preserved (Smith, 1988). The two models make very different predictions about the kinds of Upper Cambrian echinoderms that should be discovered. Under the two phase diversification model, Upper Cambrian echinoderms are numerically depauperate and were remnants of the Middle Cambrian fauna which survive through to the Early Ordovician, whereas, under the continuous diversification model Upper Cambrian echinoderms are expected to comprise intermediate taxa linking Middle Cambrian and Early Ordovician faunas.

Our collections from the Chatsworth Limestone, described here, represent the best Upper Cambrian echinoderm fauna so far reported. Although the number of Upper Cambrian species is small, they clearly bridge the gap between Middle Cambrian and Ordovician taxa. *Ridersia* is intermediate between *Gogia*-like eocrinoids and glyptocystitid rhombiferans, *Hadrodiscus* is intermediate between *Stromatocystites*-like edrioasteroids and lebetodiscid isorophids and *Cambroblastus* is intermediate between edrioasteroids and edrioblastoids. From this it would appear that echinoderms continued to diversify through the Upper Cambrian but have simply not yet been discovered, due to preservational failure. We predict that many more groups will be found to have an Upper Cambrian record when suitable fossiliferous horizons are discovered.

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